



Methyl acetate, a highly volatile floral semiochemical mediating specialized plant-beetle interactions

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Received: 3 November 2020 / Revised: 20 March 2021 / Accepted: 31 March 2021 / Published online: 2 May 2021
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Abstract

Olfactory signaling is key to the reproductive biology of entomophilous palms. Both pollinating and specialized herbivorous insects are attracted to fragrance-emitting palm inflorescences that function as reliable food sources, as well as mating and oviposition sites. In the present study, we characterized the floral scent chemistry of the acuri palm (*Attalea phalerata*), assessing its role in the attraction of flower-visiting insects associated with this species over its natural distribution range. We sampled insects from staminate inflorescences of *A. phalerata* ($n=6$) at four different sites in the Brazilian Atlantic Forest and Cerrado, and Colombian Amazon basin. Dynamic headspace scent samples of both pistillate and staminate inflorescences of *A. phalerata* ($n=3♀, 3♂$) were collected and analyzed by gas chromatography-mass spectrometry. Methyl acetate, a rare floral scent compound, was identified as the almost exclusive constituent (> 99.8% relative percentage) in all the samples. Flight-interception traps baited with methyl acetate, installed in one of the sites in the Brazilian Cerrado, were attractive to beetles associated with inflorescences of *A. phalerata* across all four sampling sites (9 spp. in total), including the putative main pollinators (*Mystrops* spp., Nitidulidae; *Andranthobius* spp., Curculionidae) and various palm borers (*Paratenthra martinsi*, Cerambycidae; *Parisoschoenus* sp.1 and *Belopoeus* sp.1; Curculionidae). Methyl acetate is highly volatile and we hypothesize its efficacy relies on profuse emission by the inflorescences of *A. phalerata*, as specialized pollinating insects respond to high concentrations of the attractant, perhaps before odor plumes rapidly disperse. Such a strategy could prove particularly effective in dense populations of *A. phalerata*.

Keywords Cantharophily · Floral semiochemicals · Derelomini · Mystropini · Palms · Arecaceae

Communicated by: John A. Byers

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Introduction

The inflorescences of palms (Arecaceae) are visited by an exceptionally diverse and abundant insect fauna (Henderson 1986). Not only are palms a predominant element in a variety of different terrestrial ecosystems (Henderson 2002); their inflorescences are often large-sized and present no morphological hindrances for easy access to a plentiful pollen food supply, as well as to sheltered mating and oviposition sites (Ervik et al. 1999; Núñez et al. 2005; Núñez-Avellaneda and Rojas-Robles 2008; Carreño-Barrera et al. 2019). Several species of insects, notably beetles, depend on the inflorescences of palm hosts in all phases of their life cycle. Adults feed, copulate, and lay their eggs within the floral microhabitats, where the larvae develop (Anderson et al. 1988; Núñez et al. 2005; de Medeiros and Vanin 2020).

Insects associated with palms commonly exhibit a narrow, specialized preference for their hosts. For instance, it is not

uncommon to observe species-specific interactions involving strictly pollen-feeding mystropine sap beetles (Nitidulidae: Mystropini) and derelomine flower weevils (Curculionidae: Derelomini), the main pollinators of the vast majority of the Neotropical Arecaceae (Henderson 1986; Núñez Avellaneda 2014). For these insects, palm inflorescences are not only their sole source of food but also their mating and oviposition sites, as the larvae are also pollinivorous (Listabarth 1996; Núñez et al. 2005). Hence, the reproductive success of dioecious and functionally dioecious beetle-pollinated palms (which encompass anywhere between 15 and 50% of the Neotropical species diversity; Núñez Avellaneda 2014) relies on the constant supply of pollen by staminate inflorescences, which are produced all year long and far more abundantly than the seasonal staminate inflorescences (Fava et al. 2011). Thus, pollination in these plant species is achieved by deception, as the oligophagous (often monophagous) pollinating beetles are driven to rewardless conspecific staminate inflorescences through a strategy of olfactory automimicry (refer to Ashman 2009). Not surprisingly, the floral scent compositions of pistillate and staminate inflorescences of many dioecious palm taxa (Ervik et al. 1999; Núñez-Avellaneda and Rojas-Robles 2008), including different species of *Attalea* (Núñez et al. 2005; Maia et al. 2018), are virtually identical. The visiting insect fauna recovered from inflorescences of both sexes for the aforementioned palm species is largely the same.

It is generally assumed that olfactory-mediated pollinator selection strongly influences the reproductive isolation of Neotropical palms. Indeed, in many instances, the inflorescences of syntopic, co-flowering palm species are visited by different sets of insects (Núñez et al. 2005; Maia et al. 2018). Volatile organic compounds (VOCs) identified in floral scents of palms include terpenoids, methoxylated aromatics, and linear alkanes (Knudsen et al. 2006; Maia et al. 2018, 2020; El-Sayed 2021). The current understanding of the floral scent chemistry of Neotropical palms is nonetheless still incipient as less than 30 and 6% of known genera and species have been investigated so far (Knudsen et al. 2006; Núñez-Avellaneda and Rojas-Robles 2008; Maia et al. 2018, 2020).

But the importance of floral VOCs in the reproductive ecology of palms extends beyond the attraction of efficient pollen vectors. Palm inflorescences constitute reliable and abundant resources in most tropical and sub-tropical ecosystems, and numerous flower-visiting insect species are drawn to them, from selective florivores and pollen robbers to miners and spermophages (Giblin-Davis 2001; Moore 2001). The activity of these insects can directly affect flowering/fruitlet fitness, as in the case of seed beetles of the genera *Caryoborus*, *Caryobruchus*, and *Pachymerus* (Chrysomelidae: Bruchinae; Moore 2001) and specialized florivorous scarabs of the genus *Cyclocephala* (Melolonthidae: Cyclocephalini; Maia et al. 2018, 2020), or increase the rates of infection/infestation by

plant-pathogenic microbes and nematodes (Moore 2001). In field bioassays, Maia et al. (2018, 2020) have successfully captured large numbers of potential pest species of *Cyclocephala* to traps baited with synthetic standards of VOCs identified in the floral scents of their palm hosts.

The acuri palm (*Attalea phalerata* Mart. ex Spreng.) is a woody palm species with solitary stems growing up to 10 m tall, but mature plants are often short-stemmed. Each individual can produce staminate, pistillate, or (rarely) androgynous inflorescences. Nonetheless, because the same individual seldom bears pistillate and staminate inflorescences simultaneously, *A. phalerata* can best be described as functionally dioecious (Núñez et al. 2005; Fava et al. 2011). Natural populations occur predominantly in forested savannas and open or disturbed areas in the Brazilian Central Plateau to southern and western parts of the Amazon region of Brazil and neighboring countries (Lorenzi et al. 2010). Plants grow either as scattered individuals or vast monodominant patches known as “acurizais” (Pott et al. 2011). Within a population, the staminate inflorescences are produced year long. Production peaks of pistillate inflorescences coincide with the beginning of the wet season, between September and November (Fava et al. 2011). The anthesis of *A. phalerata* is diurnal, with the peduncular bracts opening lengthwise to expose the flowers around 09:00 h (Fava et al. 2011). Similarly to what has been documented for other species of *Attalea* (Anderson et al. 1988; Voeks 2002; Núñez et al. 2005), Fava et al. (2011) also observed visiting insects, predominantly small beetles (Curculionidae and Nitidulidae) but also stingless bees (Hymenoptera, Apidae) and flies (Diptera, Drosophilidae), which arrive with the onset of anthesis and perceivable odor emission.

In this study, we investigated the floral scent chemistry of *A. phalerata*, assessing its potential role in attracting anthophilous (flower-visiting) insects associated with the species. We also characterized (dis)similarities in the insect fauna associated with anthetic inflorescences through a sampling effort within populations across the species' natural distribution range. We hypothesize that (i) the floral fragrance of *A. phalerata* is chemically unique when compared to those of other Neotropical palm taxa; (ii) specific VOC(s) in the floral scent of *A. phalerata* function(s) as a shared olfactory signal for highly specialized flower-visiting insects, including the species' putative pollinators; and (iii) the anthophilous insect fauna associated with *A. phalerata* is biogeographically conserved.

Materials and methods

Characterization of flower-visiting insects

We collected samples of insects from within staminate inflorescences of *A. phalerata* at four different sites covering

Table 1 Information on the four sites within the natural distribution range of the acuri palm (*Attalea phalerata*, Arecaceae) from where samples of flower-visiting insects associated with staminate inflorescences were collected. Each sample was obtained by individually enclosing a single inflorescence (from different individuals) within a clear plastic bag that was then vigorously shaken for ca. 2 min to make insects fall to the bottom. Geographical locations,

point coordinates, and elevations were obtained from Google Earth Pro 7.3.3.7786 (Google 2021). The classification of biogeographic domains follows Olson et al. (2001). Regarding the influence of human activities over the composition, balance, or function of ecological assemblages, the habitat types at the four collection sites are classified as either natural (no influence) or semi-natural (little to mild influence) (UNEP-WCMC 2014)

Location	Biogeographic domain	Habitat type	Collection date / # samples
Bonito —Balneário Municipal de Bonito, municipality of Bonito, state of Mato Grosso do Sul, Brazil (21° 10' 24" S, 56° 26' 45" W; 310 m.a.s.l.)	Cerrado	Semi-natural	March 29, 2015; 2 samples
Campinas —Instituto Agronômico de Campinas, municipality of Campinas, state of São Paulo, Brazil (22° 53' 31" S, 47° 03' 53" W; 672 m.a.s.l.)	Atlantic Forest	Semi-natural	May 16, 2019; 1 sample
Campo Grande —Praça do Rádio Clube, municipality of Campo Grande, state of Mato Grosso do Sul, Brazil (20° 27' 44" S, 54° 36' 41" W; 555 m.a.s.l.)	Cerrado	Semi-natural	May 18, 2015; 2 samples
Leticia —San Martín de Amacayacu, municipality of Leticia, department of Amazonas, Colombia (3° 47' 14" S, 70° 17' 48" W; 58 m.a.s.l.)	Amazon Basin	Natural	August 2, 2012; 1 sample

extremes of the species' natural distribution range (sensu Lorenzi et al. 2010) in the Brazilian Cerrado (2 sites), Brazilian Atlantic Forest (1 site), and Colombian Amazon basin (1 site). Regarding the influence of human activities over the composition, balance, or function of ecological assemblages, the habitat types at the four collection sites are classified as either natural (no influence) or semi-natural (little to mild influence) (UNEP-WCMC 2014; refer to Table 1 and Fig. S1 in Online Resource 1 for information).

On the morning of the first day of anthesis, between ~09:00 and 12:00 h, samples of visiting insects were obtained from 1 to 2 inflorescences chosen at random from different *A. phalerata* individuals at each of the four study sites ($n=6$ inflorescences in total; see Table 1). Each inflorescence was individually enclosed within clear plastic bags and vigorously shaken for ca. 2 min to make insects fall to the bottom (i.e., Kirejtshuk and Couturier 2010; Carreño-Barrera et al. 2020). The insects were preserved in ethanol 70%, morphotyped, and identified to the highest possible taxonomic resolution with the aid of available keys, original descriptions, and revisions (Barbosa 2001; Kirejtshuk and Couturier 2010; Casari and Teixeira 2014; Valente and Da Silva 2014), as well as comparison with material deposited in the following entomological collections: (CE-UFPE) Coleção Entomológica da Universidade Federal de Pernambuco (UFPE), Recife, Brazil (collection manager: Luciana Iannuzzi); (CERPE) Coleção Entomológica da Universidade Federal Rural de Pernambuco, Recife, Brazil (collection manager: Paschoal Coelho Grossi); and (CBUCES) Colecciones Biológicas de la Universidad CES, Medellín, Colombia (collection manager: Juliana Cardona Duque).

At three sites (*Bonito* and *Campo Grande*, state of Mato Grosso do Sul, Brazil; and *Leticia*, department of Amazonas, Colombia; refer to Table 1 and Fig. S1 in Online Resource 1), we observed the behavior of visiting insects for ~2 h following the opening of the bracts of both pistillate ($n=2$)

and staminate inflorescences ($n=3$). Based on our observations and a previous study with *A. phalerata*¹ (Fava et al. 2011) and the congeneric *A. allenii* H.E. Moore (Núñez et al. 2005), and following the classification scheme of Silberbauer-Gottsberger et al. (2013), the flower-visiting insects identified in our collected samples were characterized as (1) main pollinators—MP (i.e., those which regularly contact receptive staminate and pistillate flowers); (2) occasional pollinators—OP (i.e., those which predominantly visit either pistillate or staminate inflorescences or feed on floral resources and behave like parasites, only occasionally promoting pollination); (3) non-pollinating inflorescence visitors—IV (i.e., those which do not damage to floral structures nor legitimately pollinate pistillate flowers); and (4) parasites/pillagers—PP (i.e., those which exclusively use floral resources, never promoting pollination and often damaging reproductive structures).

For the insects categorized as MP and OP, we assigned a number for the herein identified morphospecies (not resolved until species level) and the name initials for the author of the morphospecific identification (LANA, Luis Alberto Núñez-Avellaneda). In a scenario where numerous new insect species await description, the cataloging of specimens under a preliminary but consistent nomenclature within a traceable timeframe can significantly improve basic knowledge

¹ The identity of *Attalea phalerata* Mart. ex Spreng. in a pollination ecology study published by Anderson and collaborators in 1988 is contested by specialists, as the coiled anthers of staminate flowers depicted in photos provided by the authors are uncharacteristic of the species. Morphological and biogeographical information suggest it is likely *Attalea speciosa* Mart. ex Spreng (JM Tucker Lima, personal communication). We chose not to include this study in our assessment of flower-visiting insects species associated with *A. phalerata* across its natural distribution range. Refer to Anderson AB, Overall WL, Henderson A (1988) Pollination ecology of a forest-dominant palm (*Orbignya phalerata* Mart.) in northern Brazil. *Biotropica* 20:192–205. <https://doi.org/10.2307/2388234>.

about Neotropical pollinators (e.g., distributional information), as well as better illustrate the specificity variation in interactions between insects and palms. Such an approach has already allowed the recovery of natural history observations for previously undescribed taxa (e.g., see natural history information for *Azotoctla punctata* from Franz (1999), recovered then formally described by Cardona-Duque and Franz (2012)). The nomenclature assigned to each taxon will be accompanied by high-resolution image documentation (Fig. S2 in Online Resource 1).

Floral scent sampling and chemical analysis

Floral scent samples were obtained by dynamic headspace at the *Campo Grande* site in June and October 2015 during daytime (between 08:00 and 11:00 h). Individual inflorescences, excised at the peduncle base, were fully enclosed (bract and rachis) within PET film flat oven bags (60 × 40 cm; WYDA® Assarápido Churrasco, Brazil) for 5 min. Two openings were made at opposite extremities of each bag. From one of the openings, the air enriched with VOCs inside the bags was drawn by a battery-operated rotary vane vacuum pump (model G 12/01 EB, ASF Thomas, Inc., Germany) for 30 min at a constant flow rate of 150 mL min⁻¹ and trapped in silanized glass cartridges (70 mm; 5 mm i.d.) filled with 50 mg of an adsorbent polymer mixture, consisting of equal parts of Tenax™ TA (80–100 mesh, Supelco, Bellefonte, PA, USA) and Carboxpack™ X (20–40 mesh, Supelco). Samples were taken from both pistillate and staminate inflorescences of different individuals chosen at random ($n = 5♀, 5♂$) and eluted with 150 µL hexane (99.9% chemical purity, Sigma-Aldrich USA). Because the analyses of solvent samples obtained in June 2015 were inconclusive (see the “Results” section), we used smaller cartridges (20 mm; 2.3 mm i.d.) filled with 3 mg of the adsorbent polymer mix to obtain samples for solventless thermal desorption in October 2015, taken for 5 min ($n = 3♀, 3♂$; different individuals chosen at random), according to methods described by Dötterl et al. (2005). In both sampling methods, a silanized glass cartridge filled with 50 mg activated charcoal (20–60 mesh, Sigma-Aldrich) was fitted to the other opening cut in the bag to filter incoming air. To rule out any environmental contaminant, negative controls drawn from empty bags were simultaneously collected. Although we did not control the possible influence of the excision on volatile emission, previous studies suggest it is not significant (Ervik et al. 1999; Maia et al. 2018), and cut inflorescences remain attractive to the specialized anthophilous insects.

Headspace samples were analyzed on a gas chromatograph coupled to a mass spectrometer (GC-MS; Agilent 7890A™ gas chromatograph, Agilent 5975C Series MSD™ mass spectrometer) and equipped with a non-polar HP-5 ms

column (Agilent J&W; 30 m × 0.25 mm i.d., 0.25 µm film thickness). A split/splitless inlet was fitted with an Agilent Thermal Separation Probe (TSP). For the analysis of solvent samples, 1 µL of the eluate was injected into quartz micro vials, which were then inserted in the TSP vial holder with the inlet set to split mode (1:30) and the GC injector temperature set to 250 °C. The smaller cartridges used for solventless thermal desorption were directly inserted in the TSP vial holder. The GC injector temperature set to 250 °C on split mode (1:30 for solvent samples and 1:70 for solventless thermal desorption samples). The GC oven temperature started at 40 °C for 2 min and then increased at a rate of 4 °C min⁻¹ up to 230 °C. The final temperature was held steady for 5 min. Helium (He) carrier gas flow was maintained at a constant pressure of 7.0 psi. MS source and quadrupole temperatures were set at 230 °C and 150 °C, respectively. Mass spectra were taken at 70 eV (in EI mode) with a scanning speed of 1.0 scan s⁻¹ from m/z 35–350.

A homologous series of linear alkanes (C5–C17) was used to determine linear retention indices (RIs) (van Den Dool and Kratz 1963). To determine the RIs for C7 to C17, a 1 µL aliquot of a C7–C28 solution in hexane (1000 ppm) was pipetted into a quartz micro vial and injected under the conditions mentioned above for solvent samples. Using the same method, the RIs for C5 and C6 were determined by injecting 0.3 µL of a 1:1 pentane:hexane mix (1:500 split), but we did not use a solvent cut time.

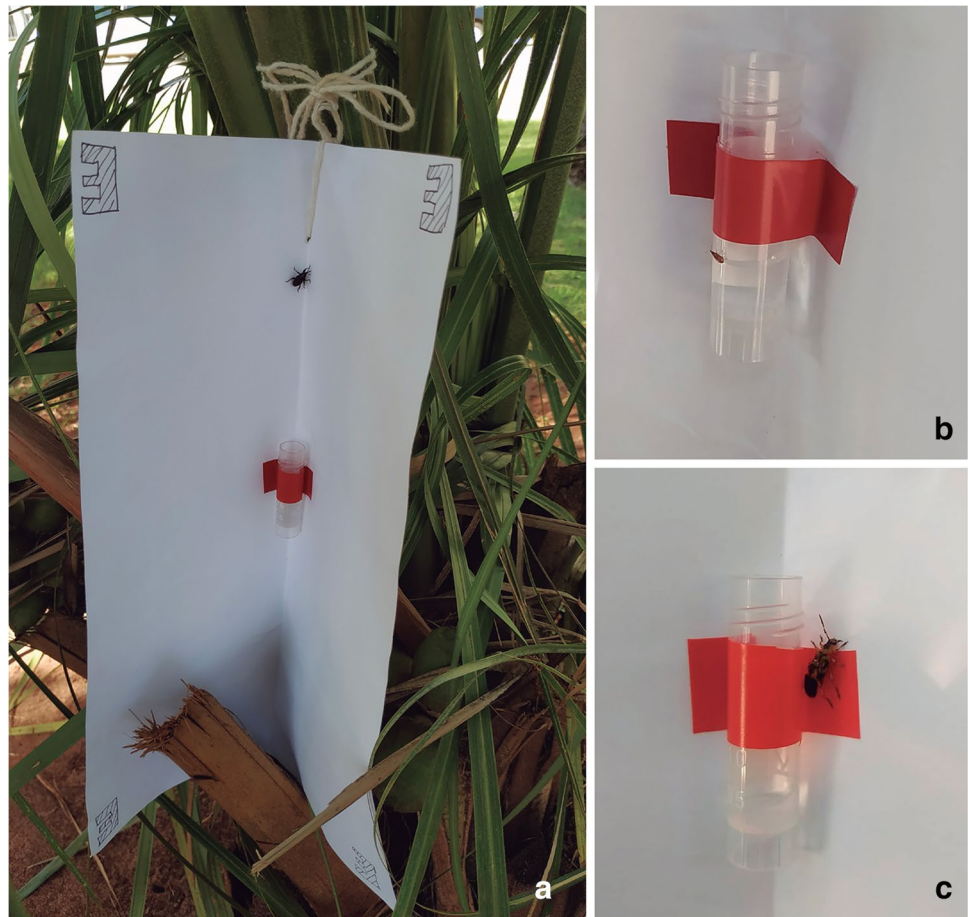
Compound identification was carried out using commercial mass spectral libraries (FFNSC 2, NIST14, and Wiley Registry™ 9th Edition), integrated into the software GCMSolution v.2.72 (Shimadzu Corporation). In order to use the original mass-chromatographic data generated in.D folder format by the MSD Chemstation software (Agilent Technologies, Inc.) in GCMSolution environment, they were first converted to compatible NetCDF (AIA/ANDI).cdf files using OpenChrom v.1.4. (Wenig and Odermatt 2010). Confirmation of the identity of the main constituent in the thermally desorbed samples was obtained by comparison with an authentic synthetic standard (methyl acetate, anhydrous, 99.5% chemical purity; Sigma-Aldrich). To quantify the total amount of this VOC in each sample of *A. phalerata*, a known aliquot (0.3 µL or 0.28 mg) of the pure synthetic standard was pipetted into a quartz microvial and analyzed in the GC–MS system under the same aforementioned conditions (1:500 split, no solvent cut time). We averaged the peak areas of three runs of the synthetic standard for comparison with peak areas of the solventless thermal desorption samples, thus estimating their methyl acetate content. The estimated total scent emissions from a single pistillate and staminate inflorescence (in mg·h⁻¹) were calculated as an extrapolation based on the content of methyl acetate in the samples and the headspace sampling interval (see above).

Field trapping bioassays

We tested the synthetic standard of methyl acetate, the main compound identified in floral scent samples of *A. phalerata*, in the selective attractiveness of anthophilous insects associated with inflorescences of this species in our study area. For field attractivity bioassays, we designed scent-baited flight-interception trapping units, each consisting of a 2 mL cryotube (KASVI®, Brazil) attached to the center of a mid-folded A4 size paper (21 × 29.7 cm, 90 gsm, white, uncoated; Fig. 1a).

On two separate occasions (June 9, 2018, and March 25, 2019) we installed sets of four traps containing 1 mL of undiluted methyl acetate, and four controls (empty open cryotubes). The traps were hung from individuals of *A. phalerata* that did not present functional inflorescences or well-developed buds. Samples of the insects intercepted by the traps or approaching them were collected with 5-mL clear glass snap cap vials (Macherey–Nagel, Germany) between 08:30 and 11:30 h, during which we also took notes on behavior and temporal patterns of arrival. We estimated the scent emissions of the loaded cryotubes ($n=5$) by applying the method used for the inflorescences of *A. phalerata* (see above).

Fig. 1 Flight-interception traps, baited with methyl acetate, set up in an urban park at Campo Grande, Central Brazil. **a** Overall appearance of the traps and attracted individual of *Belopoeus* sp.1 [LANA] (Curculionidae, Dryophthorinae). **b** Attracted individual of *Andranthobius* sp.2 (Curculionidae, Curculioninae), one of putative pollinators of *Attalea phalerata* (Arecaceae). **c** Mating couple of the longhorn beetle *Paratenethras martinsi* (Cerambycidae, Lamiinae), a borer specialized on the peduncular bracts of the inflorescences of *A. phalerata*



Vouchers of the collected insects were deposited in the following entomological collections CE-UFPE, CERPE, and CBUCES. Reference material for the investigated populations of *A. phalerata* is deposited in the following herbaria: (COAH) Herbario Amazónico Colombiano, Bogotá, Colombia (curator: Dairon Cárdenas López); COL, Herbario Nacional Colombiano, Bogotá, Colombia (curator: Jaime Uribe Melendez); CGMS, Herbário da Universidade Federal de Mato Grosso do Sul, Campo Grande, Brazil (curator: Ângela Sartori); (IAC) Herbário Fanerogâmico e Criptogâmico do Instituto Agronômico de Campinas, Campinas, Brazil (curator: Luís Carlos Bernacci).

Results

Characterization of flower-visiting insects

Collected samples at the four different sites yielded a total of 26 (morpho)species of flower-visiting insects belonging to four orders: Coleoptera (18 spp.), Hymenoptera (5 spp.), Diptera (2 spp.), and Hemiptera (1 sp.). In all samples, *Mystrops* sp.1 (Nitidulidae) was the most abundant species, followed by different species of weevils (Baridinae),

Curculioninae, and Dryophthorinae; Curculionidae) (Table 2; Fig. 2).

Ten beetle species belonging to three families were the only insects characterized as potential pollen vectors, whereas the other taxa included pollen-robbing stingless bees (*Trigona* spp., Apidae), spermophagous beetles (*Longitarsus* sp.1, Chrysomelidae), and various non-pollinating species. At least four of the putative pollinating species (*Andranthobius* sp.1 [LANA] and *Belopoeus* sp.1 [LANA], Curculionidae; *Mystrops* sp.1 [LANA] and *Mystrops* sp.2 [LANA], Nitidulidae) were abundant at three or more collection sites (Table 2; Fig. S2 in Online Resource 1).

The floral scent of *Attalea phalerata*

To our untrained noses, anthetic inflorescences of *A. phalerata* (both staminate and pistillate) at all sites emitted a strong vinegar-like aroma, detectable about 10 m away from the source. Solvent headspace samples emanated a similar fragrance on perfume test strips (IFAMIO Premium, Amazon US), but GC–MS analysis of solvent extracts did not show any mass-chromatographic peaks related to VOCs. On the other hand, all analyzed solventless thermally desorbed samples were almost exclusively comprised of methyl acetate (> 99.8% relative percentage) (Fig. 3). With a median reference retention time of 1.54 ± 0.01 (SD) min (RI 519), this compound eluted together with the large hexane solvent peak under our GC run conditions and could not be resolved in solvent headspace samples. From the solventless thermally desorbed samples, we estimated the median total scent emission of methyl acetate by a single anthetic inflorescence of *A. phalerata* between 1.9 ± 0.3 (SD) $\text{mg} \cdot \text{h}^{-1}$ (pistillate; $n = 5$) and 2.2 ± 0.4 (SD) $\text{mg} \cdot \text{h}^{-1}$ (staminate; $n = 5$). The scent of pure methyl acetate was indistinguishable from that emitted by anthetic inflorescences of *A. phalerata* when applied to a perfume test strip.

Field trapping bioassays

The median total scent emission of methyl acetate by the cryotubes was estimated at 10 ± 0.4 (SD) $\text{mg} \cdot \text{h}^{-1}$, or roughly 5 times that of an inflorescence of *A. phalerata*. A total of 132 insects were captured as they landed on or approached the flight-interception traps baited with synthetic methyl acetate. We estimate the actual number of attracted insects during the bioassays to have been two to three times larger, probably due to insects encountering the trap, recovering, and flying away. Collected specimens belong to nine beetle species, all of which also were recovered from staminate inflorescences of *A. phalerata* (Table 3). The most abundant insects in both collection dates were species of putative

pollinators, *Andranthobius* sp.1 [LANA], *Andranthobius* sp.2, *Mystrops* sp.1 [LANA], and *Mystrops* sp.2 [LANA], which together encompassed between 59.1 and 71.6% of the total number of captures in the two collection events. No insects were intercepted by or seen approaching the control traps.

Discussion

Floral scent is a central element in the pollination of *A. phalerata* across the species' natural distribution range (Lorenzi et al. 2010). The most abundant visiting insects sampled from inflorescences in all our study sites were also efficiently attracted to flight-interception traps baited with methyl acetate, the main constituent in the fragrance of both pistillate and staminate inflorescences of *A. phalerata*. The presumed effective pollinators of *A. phalerata* along its natural distribution range, mystropine sap beetles of the genus *Mystrops* and derelomine flower weevils of the genus *Andranthobius*, are exclusively associated with Neotropical palms, recorded as the main pollinators of several species among 32 and 16 genera, respectively (Núñez Avellaneda 2014). In the particular case of *Mystrops* spp. and their association with other *Attalea* species, the beetles are attracted to inflorescences by scent even several days before the actual onset of anthesis, perching over the peduncular bracts until they finally open and expose the flowers (Núñez et al. 2005). According to data from Fava et al. (2011), an unidentified species of *Mystrops* is one of two main pollinators of *A. phalerata* in the Brazilian Pantanal, based on the behavior and frequency of individuals in both staminate and pistillate inflorescences.

The conspicuous scent advertisement of the inflorescences of *A. phalerata* also appeals to other anthophilous beetles whose documented roles in association with related palm taxa do not fit that of effective pollinators (Moore 2001; Núñez et al. 2005; Silberbauer-Gottsberger et al. 2013). Less than 40% of the 26 insect species we recovered from anthetic staminate inflorescences of *A. phalerata* can accurately be characterized as pollen vectors based on predictable criteria that include their behavior, absolute abundances, and frequency, as well as their pollen-carrying capacity (Núñez-Avellaneda and Rojas-Robles 2008; Silberbauer-Gottsberger et al. 2013; Table 2). In their study on the pollination ecology of *A. phalerata* in the Brazilian Pantanal, Fava et al. (2011) restricted to only four (out of a total of 13) the number of insect species recovered from pistillate and staminate inflorescences that were likely pollinators. For instance, they documented several species of weevils (Curculionidae) belonging to the subfamilies Baridinae (2 spp.), Dryophthorinae (2 spp.), Molytinae (1 sp.), and Scolytinae (1 sp.), all of which recognized as weevil borers of palms (Giblin-Davis 2001). In our investigation,

Table 2 Insect taxa associated with anthetic staminate inflorescences of *Attalea phalerata* at four locations across the species natural distribution range (refer to Table 1 and Fig. S1 in Online Resource 1 for further details). Abundances are indicated as follows: (***) very abundant (≥ 500 individuals); (**) abundant (50–499 indiv.); (*) sporadic (5–49 indiv.); (+) rare (1–4 indiv.); and (-) absent. Visiting insect species characterized as follows: MP—main pollinators; OP—occasional pollinators; IV—non-pollinating inflorescence visitors; and PP—parasites/pillagers (refer to the “Materials and methods” section for details). In bold, species captured in flight-interception traps baited with synthetic methyl acetate (refer to the “Results” section for details)

Taxa	Role	Collection sites			
		Bonito	Campinas	Campo Grande	Leticia
Coleoptera					
Carabidae					
Lebiini sp.1	IV	+	-	-	-
Cerambycidae					
Paratenthra martinsi	IV	+	*	*	-
Chrysomelidae					
<i>Longitarsus</i> sp.1	PP	+	-	-	-
Curculionidae					
Baridinae					
Parisoschoenus sp.1	PP	*	+	+	+
<i>Parisoschoenus</i> sp.2	PP	+	+	-	+
Baridinae sp.	PP	+	+	-	+
Curculioninae					
Andranthobius sp.1 [LANA]	MP	**	+	*	**
Andranthobius sp.2	OP	-	*	*	-
Celetes sp.1	OP	*	*	+	+
<i>Celetes</i> sp.2	OP	*	*	-	-
<i>Phytotribus</i> sp.1	OP	*	*	+	+
Dryophthorinae					
Belopoeus sp.1 [LANA]	OP	**	**	*	**
Nitidulidae					
Cillaeinae					
Colopterus niger	IV	+	-	+	-
Nitidulinae					
Mystrops sp.1 [LANA]	MP	***	***	***	***
Mystrops sp.2 [LANA]	MP	**	*	**	**
Staphylinidae					
Aleocharinae					
Aleocharini					
<i>Aleochara</i> sp.1	OP	+	-	-	+
Athetini					
<i>Atheta</i> sp.	OP	+	+	-	+
Staphylininae					
<i>Xenopygus</i> sp.	IV	+	-	-	-
Diptera					
Drosophilidae					
<i>Drosophila melanogaster</i>	IV	+	+	*	+
Drosophilidae sp.	IV	+	-	-	-
Hymenoptera					
Apidae					
<i>Trigona amalthea</i>	PP	*	*	-	+
<i>Trigona spinipes</i>	PP	*	*	-	+
Formicidae					
<i>Camponotus</i> sp.	IV	+	+	-	-
Vespidae					
<i>Polybia</i> sp.	IV	+	+	-	-
Ichneumonidae					
Ichneumonidae sp.	IV	+	+	-	-
Heteroptera					
Anthocoridae					
<i>Xylocoris</i> sp.	IV	+	+	-	-

a yet unassigned species of *Belopoeus* (*Belopoeus* sp.1 [LANA]; Curculionidae, Dryophthorinae) was among the most frequent and abundant insects associated with staminate inflorescences of *A. phalerata* at all collection sites. Although Bondar (1954) reports adults of this genus as pollen-feeders and their larvae as saprophages, numerous other species of dryophthorine weevils with similar habits (Rhynchophorini and Sphenophorini) are widely acknowledged as the most damaging palm pests worldwide (Giblin-Davis 2001). We also identified two different species of *Parisoschoenus* (Curculionidae, Baridinae), a genus of weevil borers whose larvae commonly attack soft floral tissues of Neotropical palms (Giblin-Davis 2001). However, some species primarily colonize aborting fruits and therefore are not always pests (e.g., Moura et al. 2009). Both *Belopoeus*

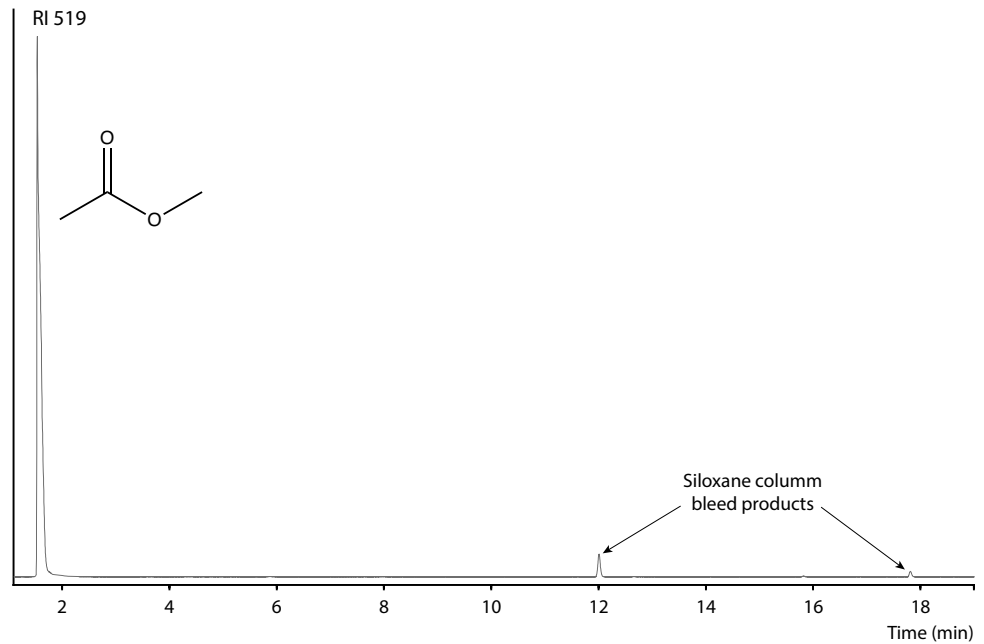
sp.1 [LANA] and one of the species of *Parisoschoenus* (*Parisoschoenus* sp.1) were attracted to flight-interception traps baited with methyl acetate.

Apart from *Mystrops* spp. and *Andranthobius* spp., the greatest number of captures with scent-baited traps ($n = 33$) was of *Paratenthra martinsi* Monné, 1998, an unusual species of acanthocinine longhorn beetle (Cerambycidae: Lamiinae: Acanthocinini). Detailed biological notes taken by Casari and Teixeira (2014) describe a scenario of potential strict dependence of this species on *A. phalerata*. Adult female and male beetles are attracted to open inflorescences, where they copulate, and the females lay their eggs on the inner face of the peduncular bracts. Throughout seven months, a single peduncular bract may exhibit over 800 exit holes made by emerged imagoes. *Paratenthra martinsi* has

Fig. 2 Flower-visiting insects associated with *Attalea phalerata* (Arecaceae). **a** Open staminate inflorescence of *A. phalerata* in the morning of the first day of anthesis. **b** Individuals of the pollinating beetle *Mystrops* sp.1 [LANA] on pollen-shedding staminate flowers. **c** Pollen-covered individual of *Mystrops* sp.2 [LANA] on the receptive stigma of a pistillate flower. **d** Various flower-visiting insect species on the inner surface of the peduncular bract of a staminate inflorescence of *A. phalerata* on the second day of anthesis



Fig. 3 Total GC–MS ion chromatogram (obtained on a DB-5 equivalent column) representative of a dynamic headspace sample from an anthetic staminate inflorescence of *Attalea phalerata* (Arecaceae). RI—linear retention index



been documented in exclusive association with *A. phalerata* in different populations within a 1100 km radius in Central Brazil (Fava et al. 2011; Casari and Teixeira 2014; this

Table 3 Total number of beetles captured with flight-interception traps baited with methyl acetate on two separate occasions (June 9, 2018, and March 25, 2019) at an urban park in the municipality of Campo Grande, Central Brazil (for further details, refer to Table 1 and Fig. S1 in Online Resource 1)

Taxa	Collection dates			
	June 2018		March 2019	
	Baited	Unbaited	Baited	Unbaited
Cerambycidae				
<i>Paratenthra martinsi</i>	24	—	8	—
Curculionidae				
Curculioninae				
<i>Andranthobius</i> sp.1 [LANA]	22	—	5	—
<i>Andranthobius</i> sp.2 [LANA]	13	—	10	—
<i>Celetes</i> sp.1	1	—	—	—
Baridinae				
<i>Parisoschoenus</i> sp.1	—	—	6	—
Dryophthorinae				
<i>Belopoeus</i> sp.1 [LANA]	—	—	2	—
Nitidulidae				
Cyllaeinae				
<i>Colopterus niger</i>	—	—	2	—
Nitidulinae				
<i>Mystrops</i> sp.1 [LANA]	20	—	6	—
<i>Mystrops</i> sp.2 [LANA]	8	—	5	—

study), so the distribution ranges of the beetle and its host plant overlap (Lorenzi et al. 2010). We hypothesize a similar scenario of insect-plant specialization and overlapping distributions for other anthophilous species recovered in our study. For instance, even though they are yet undescribed, none of the nine species of weevils (Curculionidae) found in our investigation had been previously documented in inflorescences of other palm species (Núñez Avellaneda 2014). Also relevant is the fact that five of these weevil species were recovered in inflorescences of *A. phalerata* at all four sites, which were distant from one another between 206 and 3225 km across three distinct biogeographic dominions (see Morrone 2014). The same is true for the two species of *Mystrops* (Nitidulidae).

The herein recorded *Andranthobius* sp.1 [LANA] is a new record for local Colombian faunas. Although this genus had been previously reported for the Andean natural region of the country (see Núñez-Avellaneda and Rojas-Robles 2008), it is documented for the first time in a Colombian department of the Amazon natural region and is only the second record for the Amazon region altogether (see Valente and Da Silva 2014). Additionally, although different host palms are known for the seven described species of *Andranthobius*, this is the first record of these flower weevils in palms of the genus *Attalea*. Because congeneric species within the tribe Derelomini are remarkably homogeneous in their external morphology, all recent morphotaxonomic assessments of the group are based on male (complementary female) genitalia (e.g., Valente and Da Silva 2014; de Medeiros and Vanin 2020). Internal morphology studies are being carried out to confirm whether *Andranthobius* sp.1 [LANA] is a new species.

The floral fragrance of *A. phalerata* is almost entirely constituted of methyl acetate. This contrasts with most floral scent blends across all lineages of angiosperms, which are comprised of 20–60 different VOCs (Knudsen and Gershenzon 2020). The floral scent chemistry of *A. phalerata* is also unique compared to those of other palm taxa, which usually lack aliphatic esters (Knudsen et al. 2006; Núñez-Avellaneda and Rojas-Robles 2008; Maia et al. 2018). In particular, it contrastingly differs from those of other congeners, which can be strictly dominated by mono- and sesquiterpenes (*A. allenii*; Núñez et al. 2005), methoxylated aromatic benzenoids (*A. butyracea* (Mutis ex L. f.) Wess. Boer; Maia et al. 2018), homoterpenes and 2-alkyl-3-methoxypyrazines (*A. insignis* (Mart. Ex H. Wendl.); Maia et al. 2018), and spiroketals (*A. amygdalina*; Lopera-Blair et al. 2007). Such distinct VOC profiles within *Attalea* might be an indicator of strong pollinator-mediated selective pressure among closely related palm taxa, driving rapid radiation through pre-zygotic reproductive isolation (Smadja and Butlin 2009). Sympatric co-flowering species with different floral scents, such as *A. butyracea* and *A. insignis* in the Colombian Orinoquia (Núñez Avellaneda 2014), or *A. butyracea* and *A. phalerata* in the Brazilian Amazon (JM Tucker Lima, personal communication), each present a set of flower-visiting insects distinct from one another, most noticeably from the largely abundant mystropine beetles associated with their pollination.

Methyl acetate is still poorly understood in the chemical communication of insects but has been positively tested as an attractant for blowflies (Diptera, Calliphoridae) (Camino-Lavín et al. 1996). It has also been identified as a floral scent constituent in six angiosperms species, but its function in plant-animal interactions was unknown (El-Sayed 2021). Due to its high volatility (vapor pressure 173 mmHg, 20 °C) and weak polarity, methyl acetate on GC analyses using a split/splitless injector will elute closely to most lipophilic organic solvents commonly used in headspace sampling or for obtaining flower extracts (e.g., pentane, hexane, ether, acetone, dichloromethane) (Tholl et al. 2020). It is thus not unlikely that methyl acetate as a floral scent constituent has been analytically overlooked in similar studies, as could have other naturally occurring lipophilic floral VOCs with high vapor pressures (RIs below ~675 for the solvent cut time of hexane).

We did not expect a highly volatile and structurally simple floral VOC as mediating the specialized interactions between inflorescences of *A. phalerata* and anthophilous insects. According to the literature, most semiochemicals with such characteristics are involved in alarm responses and close-contact defense, both of which rely on rapid diffusion and instant behavioral responses (as reviewed by Wyatt 2014). In communication systems where increased

selectivity is required, single-component signals often consist of complex molecular structures, which include branched chains, multiple unsaturations, oxidation, chiral carbons, and heteroatoms (Cardé and Haynes 2004). Such is the case of some unique floral scent constituents characterized by Raguso (2008) as potential mediators of “private communication channels” in plant–insect interactions, which include chiloglottones involved in deceptive pollination of *Chiloglottis* orchids by mate-searching wasps (Schiestl et al. 2003) and *trans*-carvone epoxide as a selective attractant of fragrance-seeking male bees of the genus *Eulaema* (Apidae, Euglossini) (Brandt et al. 2019). Among palms, 2-alkyl-3-methoxypyrazines function as specific attractants of cyclocephaline scarabs associated with *Acrocomia aculeata* (Jacq.) Lodd. ex Mart., *A. intumescens* Drude, *Attalea butyracea*, and *Att. insignis* (Maia et al. 2018). We hypothesize that methyl acetate functions as an effective semiochemical due to its profuse emission by the inflorescences of *A. phalerata*, so that specialized insect pollen vectors respond to high concentrations of the attractant within relatively close range. Such a strategy could prove particularly effective in naturally occurring “acurizais,” where densities of *A. phalerata* exceed 450 mature plants per hectare (Negrelle 2013), and scent trails would remain within a detectable threshold even with the rapid diffusion of the semiochemical.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00114-021-01731-3>.

Acknowledgements We thank Paschoal Coelho Grossi for helping with the processing and identification of collected insects; Letícia Koutchin Reis for valuable assistance with field bioassays; and Joanna Tucker Lima for help with the distribution map. We are also thankful to the city of Campo Grande for encouraging research and the sustainable use of urban parks.

Author contribution A.C.D.M., L.A.N., and W.A.G.N. conceived and designed the study, as well as performed the field experiments. J.C.B., L.I., and J.C.D. performed the taxonomic identifications and imaging database development. A.C.D.M. and D.M.A.F.N. analyzed the chemical data. A.C.D.M., D.M.A.F.N., J.C.B., L.I., and J.C.D. contributed reagents/materials/logistics. A.C.D.M., J.C.D., and W.A.G.N. wrote the paper. All authors read, revised, and approved the final version of the manuscript.

Funding W.A.G.N. was funded by an undergraduate scholarship awarded by CNPq (National Council for Scientific and Technological Development / PIBIC). A.C.D.M. was partially funded through grants from CAPES (Coordination for the Improvement of Higher-level Education Personnel / PNPd Postdoctoral fund) and FACEPE (Fundação de Amparo a Ciência e Tecnologia do Estado de Pernambuco / BCT-0057–2.05/17). L.I. is grateful to CNPq for her PQ2 Research Productivity Grant. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Data availability Data from the current study are available from the corresponding author upon reasonable request.

Declarations

Ethical approval This article does not contain any studies with human participants or vertebrates performed by any of the authors. The research ethics committees of the affiliated institutions have confirmed that no ethical approval is required.

Conflict of interest The authors declare no competing interests.

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