

Nocturnal and diurnal pollination in *Copaifera coriacea*, a dominant species in sand dunes of the Middle São Francisco River Basin, Northeastern Brazil

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Background and aims – *Copaifera coriacea*, a species in the resin-producing clade Detarioideae (Leguminosae), is an endemic and abundant species found in sand dunes in Brazilian Caatinga domain vegetation – a Quaternary paleodesert. We investigated floral traits and aspects of pollination biology, focusing on the pollination system of *C. coriacea*.

Material and methods – Anthesis duration, stigma receptivity, pollen viability, nectar concentration, and the presence of osmophores and pigments reflecting UV light were assessed. Floral visitors were classified as potential pollinators, occasional pollinators or thieves, based on the time and foraging behaviour and resource collected. Pollination effectiveness were assessed for potential pollinators by the detection of pollen tubes on the stigma or stylar canal by epifluorescence microscopy.

Key results – The species has white and small flowers, with anthesis beginning in the dark (ca 00:30) and the flowers are completely opened approximately 3 h later, when a sweet odour is perceptible. The onset of stigma receptivity and pollen grain viability occurs only after the completion of flower opening, and a concentrated nectar is available during the day. The presence of pollen tubes confirmed the efficiency of the main insects in the transfer of pollen.

Conclusion – Our result demonstrates that *C. coriacea* has a generalist pollination system mediated mainly by two distinct guilds of insect pollinators: moths (nocturnal, searching for nectar) and bees (diurnal, pollen collectors). This finding can provide more information about diversification in the genus *Copaifera*.

Keywords – Anthesis; floral biology; floral visitors; generalist pollination; Leguminosae; pollen tubes.

INTRODUCTION

Floral presentation (i.e. the numbers of flowers and their arrangements) and the timing of anthesis are important factors in determining and attracting pollinator guilds (Faegri & van der Pijl 1979; Fenster et al. 2004; Feldman 2006). The interactions among flowering plants and animal pollinators represent classic examples of co-adaptations conferring mutual advantages (Stebbins 1970; Faegri & van der Pijl 1979; Schemske & Horvitz 1984; Kulbaba & Worley 2012).

Such interactions were initially considered as convergent adaptations of floral attributes with effective groups of pollinators – hence the concept of “pollination syndromes” (Faegri & van der Pijl 1979; Fenster et al. 2004; Rosas-Guerrero et al. 2014). On the other hand, the existence of plant species whose flowers cannot be easily classified into any specific pollination syndrome and that have more than one effective pollen vector has given rise to the concept of a “generalist pollination system” (Waser et al. 1996; Rech

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Plant Ecology and Evolution is published by Meise Botanic Garden and Royal Botanical Society of Belgium
ISSN: 2032-3913 (print) – 2032-3921 (online)

et al. 2014). Generalist species do not have physical and/or ethological barriers to their floral resources (e.g. nocturnal and diurnal floral activity), which allows access by different pollinator guilds (Sazima et al. 1994; Avila et al. 2015; Queiroz et al. 2015; Aguilar-Rodríguez et al. 2016).

Pollinators have long been conceived of as the modulating agents of floral morphology, such that changes in pollination systems would have direct implications for plant reproductive isolation and their diversification rates (Stebbins 1970; Johnson 2010; Sapir & Armbruster 2010; Valente et al. 2012; van der Niet & Johnson 2012; Schiestl & Johnson 2013). However, a number of studies have demonstrated that the contributions of pollinators to reproductive isolation and species diversity have been overestimated (Waser et al. 1996; Sexton et al. 2013; Armbruster et al. 2014). Thus, the hypothesis of ecological isolation and/or isolation by distance (i.e. reproductive isolation by way of adaptations to contrasting environments) (Schluter 2009; Sexton et al. 2013) have been put forward in an attempt to understand diversification in those plant groups (Hughes & Eastwood 2006).

Recent phylogenies have demonstrated that the Detarioideae (Leguminosae) have a predominance of self-incompatibility mechanisms (Lewis et al. 2000) and complex patterns of floral evolution, reflected in their diversity of floral types and arrangements, as well as the presence of genera/species characterized by organ suppression (e.g. *Eperua* Aubl. with a single petal, and *Copaifera* L., which is apetalous) and reversions in relation to floral symmetry (i.e. repeated changes from actinomorphy to zygomorphy; Fougère-Danezan et al. 2010). The complex floral pattern observed in Detarioideae has been attributed to associations with a wide variety of pollinators (Lewis et al. 2000). However, in more derived groups in the subfamily with monomorphic flowers (i.e. *Copaifera*), the hypothesis that diversification attributed to interactions with different types of pollinators does not seem to be able to explain the observed infrageneric diversity.

Copaifera is a predominantly Neotropical detarioid genus, comprising ca 35 species with a conserved floral pattern (i.e. small white flowers, gathered in dense panicles; Costa 2007; de la Estrella et al. 2018). Its floral arrangement, associated with sweet odour, and pollen and concentrated nectar as floral resources, guarantee the attraction of different generalist floral visitors (Freitas & Oliveira 2002). *Copaifera* comprises many species of significant economic and ecological relevance (Mackinder 2005; Costa 2007), however, little is currently known about its floral biology and reproductive mechanisms, or if the conserved floral pattern influences the pollination systems at the species level. Detailed information is only available concerning the reproductive biology for two species of *Copaifera*: *C. langsdorffii* Desf., with wide geographic-ecological distribution, and *C. pubiflora* Benth., which is restricted to Venezuelan and Amazonian savannas, and upland and seasonally flooded forests (Ramirez & Arroyo 1990; Costa 2020). These species demonstrate diurnal anthesis and preferentially outcrossing breeding systems reinforced by self-sterility events and late acting self-incompatibility

mechanisms that result in low fruit production (Arroyo 1981; Freitas & Oliveira 2002; Oliveira et al. 2002; Costa 2007).

We investigated aspects of the pollination biology of *Copaifera coriacea* Mart., an endemic and abundant species in the continental dunes or paleodesert from the Quaternary period in the São Francisco River Basin (Rocha et al. 2004). The present study sought to describe the floral biology, and determine the *C. coriacea* pollination system. Depending on the timing of anthesis, we could expect melittophily as reported for *C. langsdorffii* (Freitas & Oliveira 2002), or a generalist pollination system as reported for *C. pubiflora* (Arroyo 1981).

MATERIAL AND METHODS

Study area

The present study was undertaken in a population of *C. coriacea* widely distributed in an area of sedimentary caatinga in the continental São Francisco dunes, municipality of Casa Nova, northern Bahia State, Brazil (fig. 1). The region has a semiarid climate (type BSh), with mean temperatures varying between 22.6°C (July) and 25.6°C (October and November), monthly precipitation varies between 1–121 mm in August and March, respectively (Alvares et al. 2013), and a high aridity index according to the FAO (AI \approx 0.28, AI = precipitation/potential evapotranspiration). Voucher specimens (*I.M. Souza* 248, 423, and 430) from each sample site were deposited in the herbarium at the Universidade Estadual de Feira de Santana – HUEFS.

Floral biology

The beginning, duration, and sequence of anthesis were observed on an hourly basis among 35 floral buds of different individuals. The number of flowers opened per individual per day was recorded. The availability of pollen grains after anther dehiscence was evaluated every two hours using a hand lens (20 \times). Floral buds and opened flowers were collected and fixed in FAA-50% every two hours for subsequent analysis and direct counting of the pollen grains under a light microscope in the laboratory (four slides per time interval; two anthers/flower) by staining with 2% acetic carmine (Nadia et al. 2013; Costa & Machado 2017). The presence of osmophores was tested for by the immersion of five flowers in 1% neutral red (Dafni et al. 2005). The presence of pigments reflecting UV light was tested for by exposing five flowers to 5% ammonium hydroxide vapours for 1 min (Scogin et al. 1977). The descriptions of the flowers were based on their collection in the field (and preservation in 70% alcohol) for subsequent dissection and stereomicroscopic analysis of their floral components.

The sugar concentrations in the nectar were measured by using a pocket refractometer (0–100% brix, Atago). Nectar was removed from the previously bagged flowers of different individuals: (i) at intervals of 30 min after completing anthesis in order to measure partial concentrations (five flowers/time interval), and (ii) at the end of the day to estimate the accumulated sugar concentration (n = 5).

Floral visitors and pollinators

Focal observations were conducted in three sample sites, along three months (during the flowering period) distributed among two flowering episodes: (i) 17–21 Feb. 2016 (04:00–17:00 on the 1st day; 02:00–17:00 on the 2nd day; 00:00–17:00 on the 3rd, 4th, and 5th day) and 13–15 Mar. 2016 (00:00–17:00 during three days); and (ii) 25–28 Jan. 2017 (00:00–14:00 during four days) – totalling 372 hours of field observation (186 h multiplied by two researchers).

Firstly, we recorded the time and foraging behaviour of the floral visitors on four individuals, the floral resource collected, and if some part of the animal's body touched the stigmatic surface. Thus, the floral visitors were classified as: (i) potential pollinators - PP, when they performed legitimate visits and touched the reproductive structures of the flowers; (ii) occasional pollinators - OP, when they performed legitimate visits but with lower intensities or at times after the peak activities of the potential pollinators; and (iii) thieves - TH, when illegitimate visits were made without touching the

reproductive structures of the flowers while collecting floral resources, without damaging the flowers (Inouye 1980).

Secondly, the “pollination effectiveness” or effective pollinator - EP (i.e. “good in terms of pollen deposition”; Ne’eman et al. 2010) was assessed for potential pollinators by the detection of pollen transfer and the presence/absence of pollen tubes (on the stigmatic surface and/or in the stylar canal) by epifluorescence microscopy. Pre-anthesis floral buds ($n = 20$) were marked and bagged in the field before anthesis. Shortly after anthesis, the bags were removed and the flowers exposed to visitors. They were bagged once again soon after receiving a single visit (moths, $n = 6$; bees, $n = 10$). Additionally, non-bagged flowers were also marked to assess natural pollination (i.e. control group; $n = 20$). All the visited flowers were fixed 24 h later in FAA-50%. The pistils were washed in distilled water, transferred to 70% alcohol, and immersed in 10N NaOH solution at 60°C for 10 min, and washed in distilled water (2 times). Clearing was performed using 2–2.5% sodium hypochlorite for 1 h, washed in distilled water (3 times), and stained with 0.20% aniline

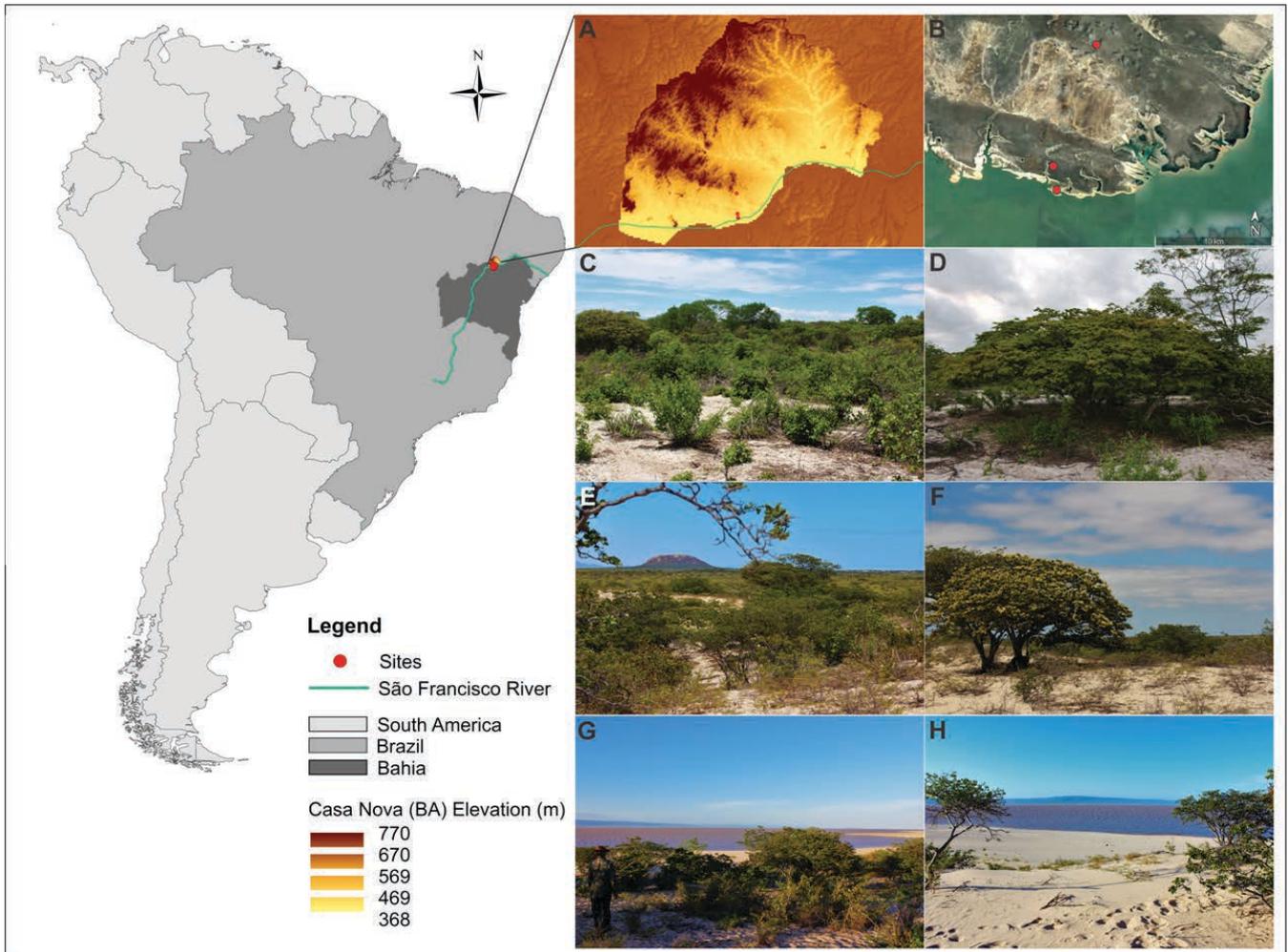


Figure 1 – Location of the *Copaifera coriacea* population studied, in the municipality of Casa Nova, in northern Bahia State, Brazil. **A.** Altitudinal variation in the Casa Nova municipality. **B.** Satellite image showing the study area in detail (source: Google Earth). **C–D.** First study site. **E–F.** Second study site. **G–H.** Third study site. Red dots = localization of the study sites on the maps. Focal individuals in first plane in the photos D, F, and H.

blue for six hours, squashed on slides to examine pollen tube growth and ovule penetration under epifluorescence microscopy (Martin 1959).

The floral visitors (insects) were collected by using an insect net and subsequently mounted and dried for identification by specialists. The specimens were deposited in the Johann Becker Entomological Collection at the Zoology Museum of the Universidade Estadual de Feira de Santana (MZUEFS), Bahia State, Brazil.

RESULTS

Floral biology

Copaifera coriacea flowers are 8 to 9 mm in diameter and displayed in panicles, with approximately 185 flowers/inflorescence. The zygomorphic symmetry is accentuated by the orientation of the flower on the axis of the inflorescence, in which the widest sepal is consistently positioned in the

direction of the apex of the axis on which the flower is inserted; four white sepals, pubescent internally; petals absent; 10 free stamens of two different sizes (ca 5 and 7.5 mm long), alternately placed, anthers whitish, with longitudinal dehiscence; pistil (ca 4 mm long) with white papillose stigma and a white style slightly curved downward in relation to the axis of the inflorescence; ovary greenish-beige, orbicular, marginally pubescent, with 1–2 ovules; green nectariferous disc at the base of the ovary (fig. 2A–F).

The floral buds initiate anthesis at approximately 00:30, with fully open flowers ca 3 hours later (fig. 3A). The stigma is receptive at the completion of anthesis (100% of the observed flowers). The anthers begin to release pollen grains around 03:30 (~50% of the flowers) and 30 min later all anthers have dehisced. Pollen viability varies between 96–98% at 03:00, and 90–95% at 06:00, with a viability decline throughout the day: 47% at 10:00 and 5% at 15:00. Sugar concentrations in the nectar vary along the day from 80% (at 04:00) to above 100% (at 08:00), and exceeds the

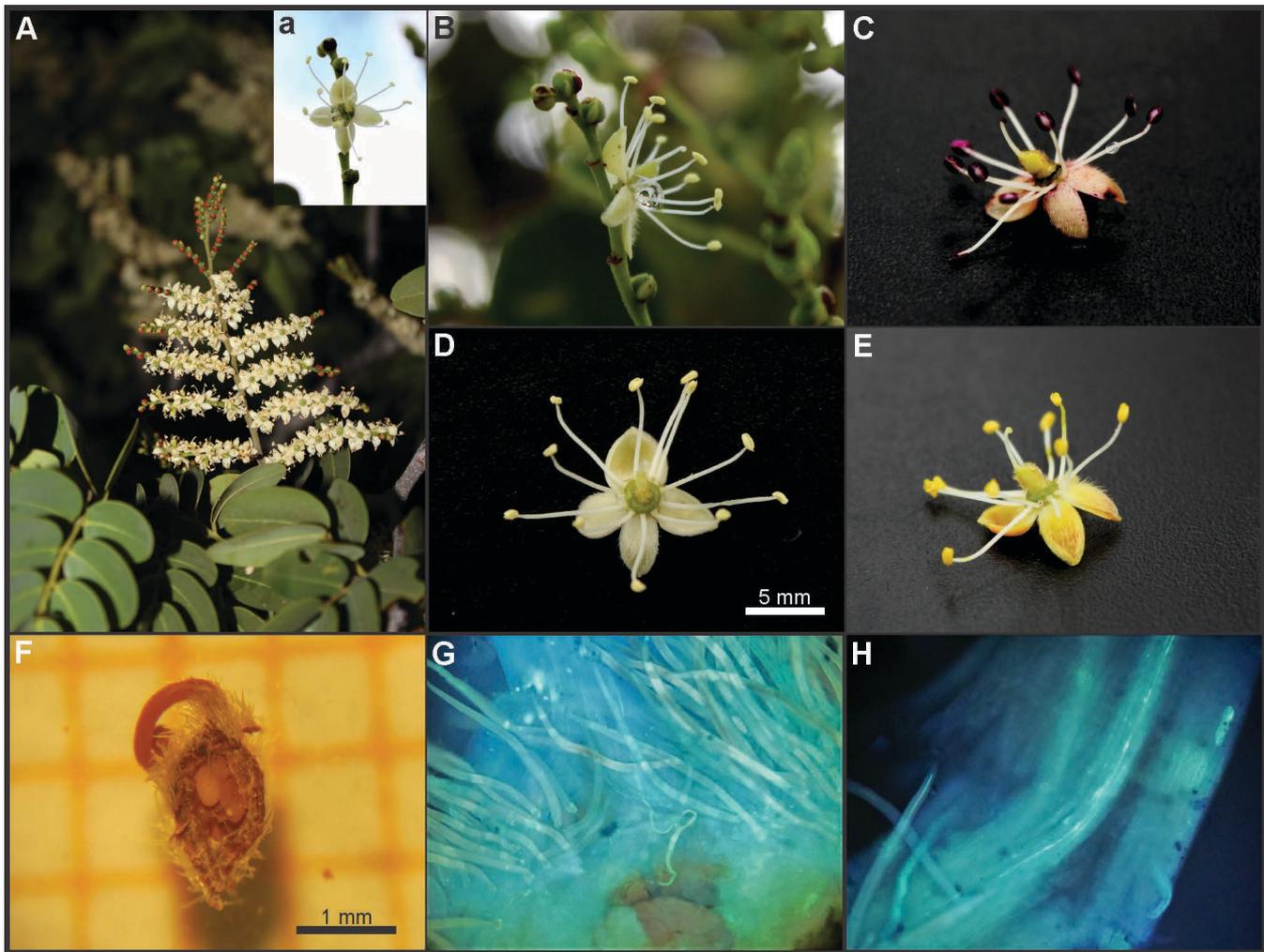


Figure 2 – *Copaifera coriacea*. **A**. Inflorescence and flower (inset a), emphasizing the orientation of the floral axis, in frontal view and in lateral view. **B**. Accumulated nectar droplets. **C**. Presence of osmophores. **D**. Detail of the flower in frontal view, showing the four sepals, stamens, green nectary, and pistil at the centre. **E**. Pigments that reflect ultraviolet light. **F**. Ovary in longitudinal section, with two marginally attached ovules. **G–H**. Results of the epifluorescence microscopy of the pollination treatments mediated by bees, focusing pollen tubes penetrating into the ovule (**G**), and pollen tubes in the canal stylar (**H**).

Table 1 – Floral visitors of *Copaifera coriacea* observed in February 2016 and January 2017 in a population growing on sedimentary caatinga in the São Francisco River continental dunes, in the municipality of Casa Nova, Bahia State, Brazil. N = nocturnal; D = diurnal; TH = thief; PP = potential pollinator; OP = occasional pollinator; EP = effective pollinator.

Order/FAMILY/Species	Visiting period	Resource	Pollen on the body	Classification
Coleoptera				
<i>Rhinochenus cf. stigma</i>	N-D	nectar	No	TH
sp.1	N-D	nectar	No	TH
sp.2	N-D	nectar	No	TH
Diptera				
sp.1	D	nectar	No	TH
sp.2	D	nectar	No	TH
sp.3	D	nectar	No	TH
Hymenoptera				
APIDAE				
<i>Apis mellifera</i> Linnaeus, 1758	D	pollen	Yes	EP
<i>Frieseomelitta doederleini</i> (Friese, 1900)	D	pollen	No	TH
<i>Melipona (Eomelipona) asilvai</i> Moure, 1971	D	pollen	Yes	EP
<i>Melipona mandacaia</i> (Smith, 1863)	D	pollen	Yes	EP
<i>Melipona marginata</i> Lepeletier, 1836	D	pollen	Yes	EP
<i>Xylocopa grisescens</i> Lepeletier, 1841	D	nectar	-	-
FORMICIDAE				
<i>Crematogaster</i> sp.	N-D	nectar	No	TH
VESPIDAE				
sp.1	D	-	No	TH
Lepidoptera				
GEOMETRIDAE				
<i>Oospila</i> sp.	N	nectar	Yes	EP
HESPERIDAE				
<i>Heliopyrgus domicella willi</i> Plötz, 1884	D	nectar	Yes	OP
LYCANIDAE				
<i>Leptotes cassius</i> (Cramer, 1775)	D	nectar	Yes	OP
NOCTUIDAE				
sp.1	N	nectar	Yes	EP
PTEROPHORIDAE				
sp.2	N	nectar	-	EP

refractometer measurable limit by the end of the day. The species has osmophores at the base of the sepals and along their edges (fig. 2C), emitting a slightly sweet odour a few minutes after completing anthesis. Pigments reflecting ultraviolet radiation were strongly present on the sepals (fig. 2E).

Floral visitors and pollinators

Copaifera coriacea attracted a wide variety of floral visitors, with insects of the orders Coleoptera (beetles), Diptera (flies), Hymenoptera (bees, ants, and wasps), and Lepidoptera (moths and butterflies) (table 1; fig. 3). Among those, moths, followed by bees, were the first floral visitors

to undertake legitimate visits, with their body sizes and/or foraging behaviour allowing contact with the reproductive structures of the flowers at times when the stigmas were receptive and pollen grains available and viable (fig. 3A).

Moths appeared between 03:30 and 05:00 and undertook short visits to few flowers (ca 4–9 flowers/crown), coming into contact with the anthers and stigma during their visits as they landed, moved about on the flowers, or circled the pistil while feeding on nectar. Bees (with the exception of *Xylocopa grisescens*, for which there was only a single recorded visit) intensely visited the crown between 05:00 and 07:00, with occasional visits later in the day. They landed on and moved about the flowers, collecting pollen, and coming into contact

with the stigma during those visits. The pollination mediated by those insects (moths and butterflies) was confirmed with the observation of pollen tubes on the stigma surfaces and in the styles and/or ovaries in 33.3% of the flowers visited by moths and 60% of the flowers visited by bees (fig. 2G, H). As such, both were classified as effective pollinators (table 1).

Butterflies also performed legitimate visits, coming into contact with the reproductive structures of the flowers as they moved around searching for nectar. Foraging activities of those insects were observed in the morning (after 08:00) and in the afternoon (near 15:00) when the anthers of most flowers were essentially empty, and the stigmas oxidized. They were therefore classified as occasional pollinators (table 1; fig. 3G).

The other floral visitors (beetles, ants, flies, and wasps) were classified as thieves (table 1; fig. 3B–F), as they undertook illegitimate visits either because of their small body sizes, which did not allow contact with the reproductive structures of the flowers (such as ants and some small Diptera), or because their foraging behaviour was inadequate

for pollination (such as flies, which visited both young and old flowers indiscriminately, and when the anthers were empty, or even absent).

DISCUSSION

Our study is the first to present conclusive evidence of the generalist pollination system in *Copaifera*, in which moths (nocturnal) and bees (diurnal) play important role in the pollination of *C. coriacea*. The set of floral attributes of *C. coriacea* match the phalaenophily syndrome (sensu Faegri & van der Pijl 1979), in which floral traits are adapted to the foraging times and energetic demands of pollinator guilds of nocturnal lepidopterans. These phalaenophilous attributes include: (i) the time of anthesis, which could to limit visitation to a specific guild of pollinators (nocturnal); (ii) the presence of odour, an important trait for guiding the pollinators to the flowers in the dark; and (iii) concentrated nectar, which restricts even more the guild of pollinators associated with the flowers. Many authors have suggested phalaenophily for plant species that demonstrate such floral

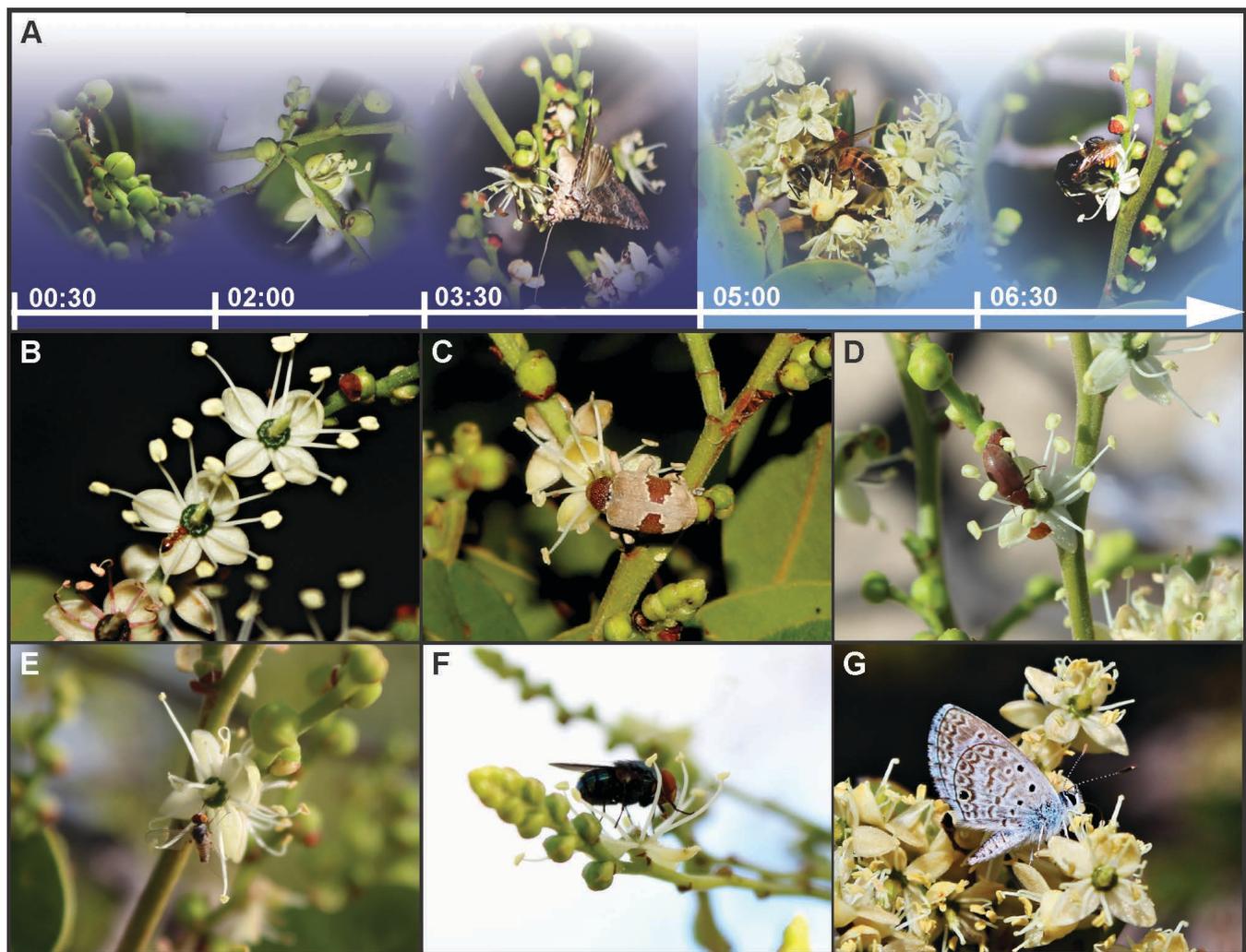


Figure 3 – Anthesis and floral visitors of *Copaifera coriacea*. **A**. Development of anthesis and the activities of moths and bees classified as effective pollinators. **B–G**. Floral visitors and pollinators searching for nectar. Ants (**B**), beetles (*Rhinochenus cf. stigma*, **C**; undetermined species, **D**), and dipterans (**E**, **F**), classified as thieves, and *Leptotes cassius*, classified as a potential pollinator (**G**).

characteristics (Faegri & van der Pijl 1979; Haber & Frankie 1989; Manning & Snijman 2002; Riffell et al. 2008; Avila & Freitas 2011). Those characteristics, in combination with receptive stigmas and viable pollen grains when moths are foraging (the first floral visitors, ca 04:00) and touching the reproductive structures of the flowers, constitute evidence of legitimate visitation, which allows classifying them as potential pollinators. Additionally, the pollination effectiveness mediated by moths was likewise confirmed by the presence of pollen tubes.

The focal species, however, also exhibited pigments that reflect ultraviolet radiation, commonly detected by diurnal insects (Primack 1982; Gronquist et al. 2001; Glover & Whitney 2010), and the flowers extend the anthesis into the day (with receptive stigmas, pollen available in the first hours of the morning, and nectar secretion). Those factors ensure the attraction of an even wider spectrum of floral visitors and allowed us to identify other pollinator guilds: (i) bees, which forage intensely in the first hours of the morning collecting pollen, and whose pollen transfer efficiency was confirmed by pollen tube formation; and (ii) butterflies, with few records of legitimate visits (i.e. touching the reproductive organs) in the morning and afternoon while searching for nectar.

Hitherto, melittophily has been attributed to *Copaifera*. For example, Rodarte et al. (2008) investigated the characteristics of the melittophilous flora of a sedimentary caatinga and included *C. coriacea* among the melittophilous species of the community based only on the floral rewards (i.e. pollen and nectar), however, they did not provide information concerning the initiation/duration of anthesis and nectar concentration. Additionally, the authors noted that *C. coriacea* was the second most-visited species by bees. In the present study, we observed the preponderance of diurnal pollination mediated by bees (i.e. 60% of flowers with pollen tube). Freitas & Oliveira (2002) classified *C. langsdorffii* as melittophilous based on its diurnal anthesis (i.e. during early morning), and pollen and concentrated nectar (49%) as floral rewards. The higher values of nectar concentration observed here (80%) may be associated with the reduction in exudates volume nectar due to the high temperatures recorded in the system (26.8°C, mean temperature of warmest quarter).

The characteristics observed in *C. coriacea* during its full floral cycle made it difficult to fit it into a single pollination syndrome. Its set of floral attributes (morphological and timing of anthesis) does not demonstrate physical and/or ethological barriers to floral resources, corresponding to a generalist pollination system. The generalist pollination system was likewise suggested for *C. pubiflora* by Arroyo (1981). Studies of pollination systems have suggested that generalist systems are more common than specialized systems, especially among species occurring in restrictive environments (such as drylands) or that experience limitations in terms of specific pollinator availability (Ollerton 1996; Waser et al. 1996; Armbruster & Baldwin 1998; Martén-Rodríguez et al. 2010). Examples such as *C. coriacea* reinforce the difficulty of defining pollination systems based on the pollination syndrome concept, as they do not always reflect the totality of floral attributes or the

spectrum of available pollinators (Ollerton et al. 2009; Avila & Freitas 2011).

The association with different floral visitors and the confirmation of effective pollination mediated by two temporally distinct pollinator guilds (moths, which are nocturnal and nectarivorous, and bees, which are diurnal and pollen collectors), indicate that *C. coriacea* has a generalist pollination system. Generalist pollination systems with the participation of both nocturnal and diurnal pollinators (in which they take on complementary roles in the sense of ensuring pollination) have been reported for other plants (e.g. *Marginatocereus marginatus* (DC.) Backeb. – Cactaceae, Dar et al. 2006; *Randia itatiaiae* Silva-Neto & Ávila – Rubiaceae, Avila & Freitas 2011; *Tillandsia heterophylla* É.Morren – Bromeliaceae, Aguilar-Rodríguez et al. 2016; *Encholirium spectabile* Mart. ex Schult & Schult.f. – Bromeliaceae, Queiroz et al. 2016), including some Leguminosae (e.g. *Calliandra longipedicellata* (McVaugh) MacQueen & H.M.Hern., Hernández-Conrique et al. 2007; *Inga sessilis* (Vell.) Mart., Amorim et al. 2013; and *Inga subnuda* subsp. *luschnathiana* (Benth.) T.D.Penn., Avila et al. 2015). However, this is the first record of a nocturnal and diurnal pollination in the genus *Copaifera*.

Stebbins (1970) noted that the pressures exerted by the most frequent and most efficient pollinators tend to become fixed in plant populations. Additionally, and depending on the animals involved, nocturnal and diurnal pollinators can exercise similar pressures on floral morphology, but, at the same time, divergent pressures on other floral traits, such as the temporal dynamics of their anthesis and nectar production (Avila & Freitas 2011). Considering that the pollinator guilds associated with *C. coriacea* are insects (small organisms with low energetic necessities), it is possible that the pressures exerted by them on floral morphology and nectar characteristics have had little (or similar) effects. That would also justify the overlapping of floral attributes seen among pollination syndromes within entomophily (e.g. odours and concentrated nectar – observed in both phalaenophily and melittophily; sensu Faegri & van der Pijl 1979).

On the other hand, the timing of anthesis tends to be a limiting factor for pollinator guilds (e.g. nocturnal anthesis associated with moths vs diurnal anthesis associated with bees; sensu Faegri & van der Pijl 1979) and, consequently, a characteristic more susceptible to selective pressures imposed by those animals. The shifting of the timing of anthesis directly implies ethological isolation in some cases, which could result in genetic divergence at the population level and, in the long-term, diversification (Grant 1949, 1994; Armbruster 2014). However, this does not seem to be the case for *Copaifera*, as even though anthesis in *C. coriacea* initiates at night (different from *C. langsdorffii*, Freitas & Oliveira 2002), its flowers remain attractive and functional even after visitation by moths, and capable of intense and effective pollination by bees in the early morning. The shifting of anthesis should not be interpreted as a speciation factor in *C. coriacea*, but rather as a mechanism that has amplified its spectrum of floral visitors/pollinators – increasing its chances of pollination in a harsh environment (Dar et al. 2006; Amorim et al. 2013; Aguilar-Rodríguez et al. 2016; Queiroz et al. 2016).

Species with generalist pollination systems tend to exhibit similar floral traits (Grant 1949), implying a conserved floral pattern that might favour overlapping of floral visitors and pollinators guilds (e.g. *C. coriacea*, in the present study; *C. langsdorffii*, Freitas & Oliveira 2002; and *C. pubiflora*, Arroyo 1981). *Copaifera coriacea* populations are geographically isolated in discontinuous sand dunes of the São Francisco watershed, in contrast to the continuous distribution of *C. langsdorffii* on a different substrate. We suggest that occupation of these distinct areas has occurred by differentiation of these species. Plant groups with monomorphic flowers and similar floral resources may have their diversification associated with environmental and/or distance isolation (Sexton et al. 2013), differently from the traditional hypothesis of diversification derived from pressures exerted by pollinator guilds (Stebbins 1970; Armbruster & Baldwin 1998; Fenster et al. 2004; Johnson 2010; van der Niet & Johnson 2012; Gómez et al. 2014).

CONCLUSION

The attraction of different insects has been reported for other species of *Copaifera* (e.g. *C. langsdorffii*, classified as melittophilous; Freitas & Oliveira 2002) and might reflect the monomorphic floral pattern of the genus (i.e. small and white flowers, without barriers to pollen and nectar, gathered in dense inflorescences). However, the evidence of pollination effectively mediated by nocturnal and diurnal pollinator guilds points to a generalist pollination system for *C. coriacea*. This mechanism amplifies the spectrum of floral visitors/pollinators of *C. coriacea*, increasing its chance of pollination in a harsh environment, with implications for the reproductive success, as reported for other plant species (e.g. Dar et al. 2006; Avila & Freitas 2011).

ACKNOWLEDGEMENTS

The authors would like to thank the Universidade Estadual de Feira de Santana for providing the infrastructure necessary to process and analyze the field data; Dr Favízia F. de Oliveira and Dr Patrícia Rebouças for identifying the bee species; Dr Thamara Zacca for identifying the lepidopterans; and the residents (Mr Antônio Borges Barreto and family) of Fazenda Santarém, Casa Nova, Bahia for their hospitality and logistic support during the field activities. In addition, two anonymous reviewers and the associate editor provided numerous comments that improved a previous version of this manuscript. This study was partially financed by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001: IMS was supported by a CAPES grant. FMH was supported by a CNPq- 302381/2020-1 grant. LPQ was supported by a CNPq-Pq1A grant.

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- Communicating editor: Renate Wesselingh.
- Submission date: 27 Jan. 2020
Acceptance date: 25 Jan. 2021
Publication date: 24 Jun. 2021