Flowering phenology of *Mouriri guianensis* (Melastomataceae) and its interaction with the crepuscular bee *Megalopta amoena* (Halictidae) in the restinga of Lençóis Maranhenses National Park, Brazil

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ABSTRACT

Mouriri guianensis is a Brazilian endemic plant species distributed throughout the Amazon forest, Caatinga, Mata Atlântica and Cerrado domains, extending northward into Venezuela. The aim of this study was to describe the flowering phenology, floral biology and visitors associated with *M. guianensis*, highlighting the crepuscular bee species *Megalopta amoena*. *Mouriri guianensis* flowers from September to March. The flowering, the details of floral biology and the activities of floral visitors were observed for ten individual plants in December 2013, January-March 2014, September-December 2014 and January-March 2015. The flowering peaks occurred in December 2013 and in November-December 2014. Bees were collected in January and February 2015. A total of 86 individuals belonging to six bee species were recorded visiting the flowers, with *Xylocopa cearensis* making more than one-half of the visits (60%), followed by *Melipona subnitida* and *Megalopta amoena* with 21.17% and 9.41% of the visits, respectively. The visitors showed activity peaks between 5:00 and 6:00 AM (66.27%). Buzz pollination was their predominant behavior. *Megalopta amoena* used its jaws to open the pore and the anther gland. *Melipona subnitida* used parts of the glands to seal the entrance to the colony. The visitors, except for *Augochlopsis* sp. and *Trigona* sp., are pollinators of *M. guianensis*. Plants having an extended anthesis can attract visitors both day and night. In this study, we present an example of a crepuscular pollination system. We suggest that blooming at twilight is a strategy used by the plant to escape unsuitable visitors.

KEYWORDS: Pollination, insect-plant interaction, floral oil, crepuscular foraging.

Fenologia da floração de *Mouriri guianensis* (Melastomataceae) e sua interação com a abelha crepuscular *Megalopta amoena* (Halictidae) na restinga do Parque Nacional dos Lençóis Maranhenses, Brasil

RESUMO

Mouriri guianensis é uma espécie vegetal endêmica do Brasil, distribuindo-se pelos domínios da Floresta Amazônica, Caatinga, Mata Atlântica e Cerrado, chegando ao norte até a Venezuela. O objetivo do estudo foi descrever a fenologia de floração, a biologia floral e os visitantes florais de *M. guianensis*, com destaque para as abelhas crepusculares *Megalopta amoena. Mouriri guianensis* floresce de setembro a março e a floração de dez indivíduos foi acompanhada em dezembro/2013, janeiro-março/2014, setembro-dezembro/2013 e novembro-dezembro/2014. As abelhas foram coletadas em janeiro e fevereiro de 2015. Um total de 86 indivíduos de seis espécies de abelhas foi registrado visitando as flores com *Xylocopa cearensis* realizando a maioria das visitas (60%), seguida por *Melipona subnitida* e *Megalopta amoena* com 21,17% e 9,41%, respectivamente. Os visitantes mostraram picos de atividade entre 5:00 - 6:00 h (66,27%). O comportamento predominante foi o de vibração. *Megalopta amoena* utilizou suas mandíbulas para romper os poros da antera e glândula. *Melipona subnitida* utilizou partes das glândulas para a vedação da entrada da colônia. Os visitantes, a exceção de *Augochlopsis* sp. e *Trigona* sp., são polinizadores de *M. guianensis*. Plantas com longos períodos de antese podem atrair visitantes diurnos e noturnos. Aqui demonstramos um exemplo de sistema de polinização crepuscular, sugerindo que o fato florir durante o crepúsculo é uma estratégia da planta para escapar de visitantes inoportunos.

PALAVRAS-CHAVE: Polinização, interação inseto-planta, óleo floral, forrageamento crepuscular.

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INTRODUCTION

Plant-pollinator interaction involves reciprocal adjustments between interacting participants, ultimately leading to interspecific mutualisms or "guild coevolution" (Thompson 1989). The interactions can be studied from combined phytocentric and zoocentric perspectives to identify and understand the pollination syndromes, plant reproductive success, floral visitors, associated behaviors and pollination efficiency (Martins 2013; Freitas *et al.* 2014).

Floral resources generally mediate the relationship between flowers and visitors. For example, pollen is an essential resource for feeding bees and is also essential in plant reproduction; these two functions are mutually exclusive (Westerkamp 1997; Agostini *et al.* 2014). The plants must allocate pollen grains to reproduction. They also need bees for pollination, a conflict termed the "*pollen dilemma*" (Westerkamp 1997).

Accordingly, plants need to make functional adjustments to maintain their visitors. A few examples, among many possible adjustments, are the production of large amounts of pollen grains in the case of "*pollen of flowers*" (Cruden 2000) and the spatial separation of stamens (heteranthery) present in *Senna, Cassia, Chamaecrista* and *Tibouchina* flowers that can guarantee efficient resource allocation and ensure reproduction (Vogel 1974; Buchmann 1983; Vallejo-Marin *et al.* 2009). Additionally, poricidal anthers, which can provide adaptive advantages to the plant by minimizing pollen harvesting by less efficient visitors (Buchmann 1983), and nocturnal anthesis, in certain species such as *Mouriri*, could be strategies that facilitate the avoidance of unsuitable visitors (Wcislo *et al.* 2004).

Mouriri is a Neotropical genus that shows the '*buzz* pollination' syndrome, with an absence of nectar in its flowers. However, in addition to providing pollen to its visitors, small epithelial elaiophores are located on its anthers. These structures produce a nonvolatile oil whose specific ecological function of which for the bees remains unknown (Buchmann and Buchmann 1981; Agostini *et al.* 2014). *Mouriri* flowers are associated with visitors that are diurnal foragers, including bees belonging to the genera *Xylocopa, Trigona, Melipona* (Buchmann and Buchmann 1981) and *Centris* (Oliveira 2010), which are among their main pollinators.

Most bee species are active during the day. However some of them, such as *Megalopta* (Halictidae, Algochlorini), are adapted to a restricted niche, foraging at twilight, when most bee species are not active (Wcislo *et al.* 2004; Warrant *et al.* 2006; Wcislo and Tierney 2009). The aim of this study was to describe the flowering phenology, floral biology and the visitors of *Mouriri guianensis*, highlighting the crepuscular bees *Megalopta amoena*.

MATERIALS AND METHODS

The present study was conducted in an area of *restinga* within the Lençóis Maranhenses National Park (LMNP), at the settlement Ponta do Mangue (2°58'12" S; 42°79'56" W), Barreirinhas, Maranhão, Brazil. LMNP has an area of 155.000 ha, with 453.28 km² covered by vegetation, 405.16 km² of which are predominantly *restinga*. Mangroves and river bank communities (riparian forests) are also still present in the park (Brasil 2002). The climate of the region is megathermic tropical (Aw' Type, according to the Köppen classification). The mean annual temperature is between 26 and 27 °C. The annual rainfall ranges between 1600 and 1800 mm, with two well-defined seasons: rainy from January to July and dry from August to December (Brasil 2002).

The phenology of ten *Mouriri guianensis* Aubl. (Melastomataceae) individuals was followed on a fortnightly basis during the study periods December 2013 to March 2014 and September 2014 to March 2015. For the purposes of this study, we have defined the flowering period from the time of the initial formation of the bud until the time that the flowers reach senescence. The periods during which a relatively large number of flowers were in anthesis were considered as the flowering peaks (Newstrom *et al.* 1994). The collected botanical material was deposited at the Herbarium of the Federal University of Maranhão - MAR.

The flowering pattern of the species was ranked by using the Fournier scale (Fournier 1974), which estimates the intensity of each phenophase in a semi-quantitative manner based on gaps and five categories (0-4). Zero quantity indicates phenophase absence; 1- phenophase presence with a magnitude ranging from 1 to 25%; 2- from 26% to 50%; 3- from 51% to 75% and 4- from 76% to 100%. Every month, the sum of the phenologic intensity values for all individuals was calculated and divided by the maximum possible value (number of individuals x 4). The value obtained was expressed as a percentage (Bencke and Morellato 2002): Fournier (%) = Σ phenophase x 100 / N x 4. Spearman's correlation (with a 95% confidence interval) was used to analyze the relationship between meteorological factors (temperature, relative humidity and rainfall) and flowering.

Monthly meteorological data (temperature, relative humidity and rainfall) were provided by the Meteorologic Laboratory/Climatological and Environmental Center of the Maranhão State University (Laboratório de Meteorologia/Núcleo Geoambiental da Universidade Estadual do Maranhão (LABMET/NUGEO). Data on anthesis onset, sequence and duration, the number of buds and open flowers per day, the type of reward offered to the visitors, floral longevity and odor emission were obtained in the peak flowering months.

Direct observations of the bees were performed by verifying the visitor type, the harvested reward, the pollen deposition site and the hourly timing and duration of visits. The counts of the number of visits were made based on the number of times the bee alighted on the flowers to harvest the reward. At each hour associated with a collection event, the behavior of the visitor was followed for 15 minutes by taking notes, filming and photographing (Nikon D90, Nikon Corporation, Tokyo, Japan).

The temperature and daily relative humidity were obtained with a digital thermohygrometer (model 7666.02.0.00, Incoterm, Porto Alegre-RS, Brazil). Measurements were made at one-hour intervals.

Floral visitors were collected in January and February 2015 with the use of an entomological net, at first from 6:00 AM to 18:00 PM and then from 18:00 PM to 6:00 AM, for five successive and three full-moon days in January 2015 to cover the entire whole nocturnal visitation period. Later, the observations were made from 04:00 AM to 18:00 PM during 10 non-consecutive days in February 2015. The collected bees were deposited in the bee collection of the Federal University of Maranhão - LEACOL.

To identify the plant species in addition to *M. guianensis* that were visited by *Megalopta amoena* Spinola throughout the sampling period, the pollen loads from five individuals were acetolyzed using Erdtman's method (Erdtman 1960).

RESULTS

Flowering in *M. guianensis* occurs from September to March (Figure 1). December 2013 and November/ December 2014 showed relatively large numbers of open flowers. The number of buds was higher from September to January (Figure 1). Flowering showed a significant correlation with relative humidity ($r_s = -0.7545$, p = 0.0015for buds; $r_s = -0.7149$, p = 0.0018 for flowers). However, temperature ($r_s = 0.2036$ and p = 0.4495 for buds; $r_s =$ 0.1653 and p = 0.5406 for flowers) and rainfall ($r_s = -0.1726$ and p = 0.5226 for buds; $r_s = -0.0136$ and p = 0.9601 for flowers) were not significantly correlated with the studied phenophases.

The *M. guianensis* plants examined in this study are shrubs nearly 1.5 m tall possessing white, pentamerous flowers and stamens with yellow, dithecal, poricidal anthers, with elaiophores on their upper part. The stamens are positioned so that the apical pores of the anthers maintain a position in which they are turned downward toward the stigma (Figure 2). The flowers show, on average, seven buds/inflorescence (7.6 \pm 4.5) and from two to three open flowers per day. The flowers offer pollen and oil as rewards. The odor originates from the anthers, calyx and corolla and is strong during the night and until the early morning. Blooming begins at approximately 18:00 PM with the gradual separation of the petals and is over by approximately 4:00 AM. Floral longevity is short, and by approximately 9:00 AM, the flower already holds anthers bearing no pollen and darkened elaiophores.

We recorded a total of 86 individuals from two subfamilies and six species of Apidae in approximately 250 hours of observation. *Xylocopa cearensis* Ducke conducted more than half of the visits (60%), followed by *Melipona subnitida* Ducke and *Megalopta amoena* with 21.17% and 9.41% of the visits, respectively (Table 1).

Megalopta amoena bees were the first visitors, starting their foraging activity approximately 5:00 AM and ending it at 5:35 AM, visiting few flowers and remaining in them for nearly 23 seconds (22.9 ± 1.19). No visits of this species were observed at any other time.

The sampling of the pollen load found in the scopes of *M. amoena* showed 88.5% from *M. guianensis* and 17.6% belonging to other plant species [6% *Machaerium* type (Fabaceae), 4% *Protium heptaphyllum* (Aubl.) March (Burseraceae), 2% *Mimosa misera* Benth. (Mimosaceae), 1.5% *Astrocaryum* sp. (Arecaceae), 1% *Anacardium microcarpum* Ducke (Anacardiaceae), 1% *Myrcia obtusa* Shauer (Myrtaceae), 1% *Xyris paraensis* Poepp. (Xyridaceae), 0.6% *Hyptis* type (Labiateae), 0.5% *Tabebuia* type (Bignoniaceae)].

Melipona subnitida bees began their activities at 5:30 AM and ended at approximately 8:00 AM, while *Xylocopa (X. cearensis* and *Xylocopa grisescens* Lepetelier) bee species initiated their harvesting activities at approximately 6:00 AM. As a whole, the visitors concentrated their activity peaks between 5:00 AM and 6:00 AM (66.27%) (Figure 3). Except for *M. amoena*, these other bee species remained on the flowers for nearly three to four seconds. Spearman's correlation analyses did not demonstrate significant associations between abiotic factors and bee activities ($r_s = -0.38$ and p = 0.1929 for temperature; $r_s = 0.46$ and p = 0.1083 for relative humidity).

Buzzing was the predominant harvesting behavior for all studied bees. The collected bees showed no effective floral oil harvesting, and the common specialized bees that harvest floral oil (*Centris, Epicharis, Tetrapedia* or Tapinotaspidini) were not observed. Nevertheless, *M. amoena*, in addition to the "*buzz pollination*" behavior (Figure 4 A-D), alighted on the flower, clinging to just one stamen, utilizing its strong jaws to open the anther

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Months

Figura 1. Relationship between flowering phenology (buds and flowers) of *Mouriri guianensis* Aubl. and abiotic factors (temperature, relative humidity and rainfall), Lençóis Maranhenses National Park, Maranhão, Brazil. A) Rainfall, temperature and relative humidity. B) Flowering.

Table 1. Visiting bees of Mouriri	quianensis Aubl. on	restinga Lencóis	Maranhenses National Park	Maranhão Brazil

Family/Tribe/Species	Individuals	(%)
APIDAE		
Meliponini		
Melipona (Melipona) subnitida	18	21.17
Trigona sp.*	1	1.17
Xylocopini		
Xylocopa (Neoxylocopa) cearensis	51	60
Xylocopa (Neoxylocopa) grisescens	6	7
HALICTIDAE		
Augochlorini		
Megalopta (Amoena) amoena	8	9.41
Augochloropsis sp.	2	2.3

*not collected species

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Figure 2. (A) Mourini guianensis Aubl. flower. (B) General aspect; (C) Anthers indicating apical pore (P) and oil gland (GL), Lençóis Maranhenses National Park, Maranhão, Brazil. Scale bars = 3 mm (A), 20 cm (B) and 10 mm (C). This figure is in color in the electronic version.



Figure 3. Relationship between *Mouriri guianensis* Aubl. and bees visiting hours with daily temperature (°C) and relative humidity (%), Lençóis Maranhenses National Park, Maranhão, Brazil. A) Relative humidity and temperature. B) Percentage of visiting bees.

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Figure 4. Harvesting behavior exhibited by *Megalopta amoena* Spinola on *Mouriri guianensis* Aubl. flowers, Lençóis Maranhenses National Park, Maranhão, Brasil. (A, B, C, D) Pollen harvesting through buzz pollination. (E, F) Bees breaking up the region of the apical pores and glands of the anthers. Scale bars = 6 mm (A, C, D, E, F) and 4 mm (B). This figure is in color in the electronic version.

pores and, at times, breaking up the oil gland (Figure 4 E-F), suggesting that this species could show facultative pollen theft.

Melipona subnitida bees harvested pollen from M. guianensis and utilized their gland regions to sealing the colony entrances (the colonies were located in nearby manmade boxes) (Figure 5 A-B). We found that the entrance to the boxes was sealed during the night and reopened only by morning (Figure 5 C-D). One individual of the genus Trigona was observed harvesting pollen straight from the anthers without contacting the stigmas and scraping the glands with its middle legs. However, this species was not collected. Augochloropsis sp. was only observed flying over the flowers.

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Figure 5. Entrance structure of one man-made box of Melipona subnitida Ducke. (A) Entrance of the box. (B) Box entrance sealing. (C, D) Box entrance open. Arrows showing *M. guianensis* anthers. Scale bars = 10 mm (A), 20 mm (B), 15 mm (C, D). This figure is in color in the electronic version.

DISCUSSION

Abiotic factors such as temperature, humidity and rainfall influence the induction and control of flowering and, consequently, activity and interaction with pollinators (Knoll and Santos 2012). In this study, it was noted that with the exception of relative humidity, meteorological factors were not significant in relation to flowering. This could be due to the absence of large fluctuations in monthly temperature averages and precipitation during the studied period. In low-seasonality environments (uniform climates), climatic factors influence the flowering of species in a less obvious way (Locatelli and Machado 2004).

Spearman's correlation analysis involving relative humidity showed that as this climatic variable decreases, flowering increases. In periods of low humidity, the plants increase their evapotranspiration rates considerably, consequently increasing soil water and nutrient input and thereby ensuring that energy reserves are adequate (Odum 1971; Locatelli and Machado 2004). Given the characteristics of the studied area, this may be a physiological strategy used by *M. guianensis* to ensure adequate energy reserves. Thus, in addition to climatic factors, physiological factors can influence flowering (Locatelli and Machado 2004).

Although *M. guianensis* flowers attracted bees with diurnal foraging habits such as *Xylocopa* and *Melipona* as their more common visitors, nocturnal anthesis and the emission of strong odors during the night represent major attractants for bee species such as *M. amoena* that pollinate flowers based on a pattern of nocturnal or crepuscular melittophily.

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Two crepuscular bee species (*Megalopta sodalis* Vachal and *Ptiloglossa aff. dubia* Moure) were found visiting the flowers of *Cambessedesia wurdackii* Martins, Melastomataceae. Although this plant was sought by diurnal visitors, crepuscular bees were found to be its potential pollinators (Franco and Gimenes 2011).

Plants with an extended anthesis, more than 12 hours, attract diurnal and nocturnal visitors, both of which are effective pollinators of the visited plants (Martins 2013; Aguilar-Rodriguez *et al.* 2015). A similar result was found in this study, suggesting that bees that visit *M. guianensis* can play a complementary role in pollination (Martins 2013; Aguilar-Rodriguez *et al.* 2015).

Megalopta amoena starts to forage on flowers before other bees. Accordingly, considering that *M. amoena* has large and robust bees, such as *X. cearensis* and *X. grisencens*, as its main competitors in the study area, its pattern of foraging during the period where the other pollinators are not active increases the reward harvested, reducing the chances for competition and predation (Wcislo *et al.* 2004).

In contrast, an interesting idea about the resource partitioning and resource sharing is "*sensory exclusion*", where interactions occur in sensory windows to which less efficient members may not have access (Lunau *et al.* 2011; Brito *et al.* 2014). Red flowers pollinated by hummingbirds, for example, represent a color niche that only hummingbirds can identify, as these flowers are inconspicuous to bees (Lunau *et al.* 2011). This study appears to furnish an example of an interaction mediated by this principle, suggesting that the blooming of the plant at twilight is a strategy to escape from undesirable visitors.

Several studies have previously confirmed that *Megalopta* are active on plants with poricidal anthers (Wicslo *et al.* 2004; Franco and Gimenes 2011). Species with diurnal and/or nocturnal anthesis belonging to Anacardiaceae, Bombacaceae, Guttiferae and Melastomataceae were identified as plants that served as a pollen source for *Megalopta* bees (Wcislo *et al.* 2004; Smith *et al.* 2012). Analysis of the pollen loads carried by *M. amoena* suggests that, although *M. guianensis* had been responsible for 88.5% of the pollen, they also visited many other plant species to harvest this pollen reward, confirming the diffuse nature of most established relationships between plants and pollinators (Martins 2013).

The higher visitation rate of *X. cearensis* to the flowers in the study area may be explained by the observation that *Mouriri* was the possible source of pollen for this species. *Xylocopa* bees utilize pollen as food (Viana *et al.* 2002) and *M. guianensis* is a plant with abundant pollen. In addition, *Xylocopa* are efficient pollination agents, mainly for plants such as *Mouriri* with poricidal anthers (Buchmann 1983). Poricidal anthers could be a strategy for avoiding the harvest of pollen grains by less

efficient visitors (Junker and Blüthgen 2010; De Luca and Vallejo-Marin 2013), reducing the numbers of visiting bees, as found in *Tibouchina, Comolia* and *Mouriri* (Buchmann and Buchmann 1981; Buchmann 1983; Oliveira-Rebouças and Gimenes 2004). Furthermore, the large quantity of pollen produced and the heteranthery presented by *Mouriri* flowers may, in part, contribute to mitigate the problem of the "*pollen dilemma*," guaranteeing their reproductive and feeding success (Vallejo-Marin *et al.* 2009).

The high visitation rate of *Melipona subnitida* is due to the location of the harvesting area in the immediate proximity of man-made colony boxes as well as the availability of larval food (pollen) and material (oil) for sealing the colony entrance from the plant. Siqueira *et al.* (2007), analyzing several stingless bee species nests, found their entrances to be mainly composed of plant resins and animal feces. The presence of resins in *Mouriri* species and the exploitation of the glands of these species by *Melipona* bees have previously been observed (Buchmann and Buchmann 1981). The present work shows evidence that *M. subnitida* utilizes *M. guianensis* floral oil. The sealing of the entrance at night and reopening in the morning occurred in a pattern similar to that seen in other Meliponinae such as *Tetragonisca angustula* Latreille (Cortopassi-Laurino and Nogueira-Neto 2003).

Although Meliponinae are specialized in harvesting floral resins for building the wall of their nests (Agostini et al. 2014), their harvesting of floral oils from Mouriri flowers has already been reported (Buchmann and Buchmann 1981; Renner 1984). Trigona pallens Fabricius were observed on the elaiophores of Mouriri myrtilloides subsp. parvifolia (Benth.) Morley in Panamá (Buchmann and Buchmann 1981). The behavior of scraping the floral connective glands to harvest the oil that would probably be mixed with pollen has been observed in Trigona williana Friese, Melipona fulva Lepeletier and M. marginata Lepeletier, whereas nine species (six Euglossa and three Xylocopa) only harvested pollen (Renner 1984). Most likely, the oil harvesting makes it easy for the pollen grains to adhere to the smooth ventral surface of these bees and increases the amount of rewards to be carried (Rêgo and Albuquerque 1989).

The flowers of *M. guianensis* produce an odor that is strongly emitted during the night. Thus, the bees capacity to detect smells may have an important role in searching for flowers at twilight conditions (Knoll and Santos 2012). Most likely, bees use these floral scents to help them with the location of pollen sources, an important factor for foraging bees in low-light conditions (Dobson and Bergström 2000; Wcislo *et al.* 2004).

The flowers of *M. guianensis* secrete an aromatic oil used by the visiting bees. However, the oil from *Mouriri* could not be viewed as a floral reward because its ecological functions Flowering phenology of *Mouriri guianensis* (Melastomataceae) and its interaction with the crepuscular bee Megalopta amoena (Halictidae) in the restinga of Lençóis Maranhenses National Park, Brazil

for the bees exploiting it remain not fully defined; so far as we know, it only serves to facilitate the adherence of pollen grains to the thorax of the *Epicharis* and *Trigona* bees (Buchmann and Buchmann 1981; Steiner 1985; Agostini *et al.* 2014). Although no floral oil harvesting-specialized bee species, such as Centridini, Tapinotaspidini and Tetrapediini, were found visiting *M. guianensis* flowers, evidence of the exploitation and use of the oil from *Mouriri* flowers by their visiting bees (*Trigona* sp., *M. amoena* and *M. subnitida*) was observed; thus, this oil appears important to them.

Visiting bees, apart from *Augochloropsis* sp. and *Trigona* sp., were considered potential pollinators of *M. guianensis*, considering their harvesting behaviors and body sizes. While they vibrate, bees hold themselves to a group of stamens, bending their entire bodies over it, shortening the distance to the stigma and transferring pollen grains.

CONCLUSIONS

From our results, we conclude that *M. guianensis* is an important source of resources for the pollinating bees that collect pollen via the specific vibration mechanism known as buzz pollination. Additionally, evidence for the use of oil by *M. subnitida* characterizes *Mouriri* as important species for these bees in the study area. Additionally, this plant species, despite being associated with the daytime visits of bees, attracts and is pollinated by crepuscular bees, presenting a case of a crepuscular pollination system. Thus, we suggest that both daytime and nighttime visitors can act in a complementary manner in the pollination process. However, further studies are needed to confirm this hypothesis. Finally, the data of the present study will serve to strengthen knowledge about *Mouriri* as well as about the mechanisms related to plant interaction and crepuscular bees.

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