SCIENTIA PLENA VOL. 20, NUM. 05 2024
www.scientiaplena.org.br doi: 10.14808/sci.plena.2024.051201

Pollination biology of *Humiria balsamifera* var. *floribunda* (Humiriaceae) on the coast of Maranhão, Brazil

Biologia da polinização de *Humiria balsamifera* var. *floribunda* (Humiriaceae) no litoral do Maranhão, Brasil

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(Recebido em 16 de julho de 2023; aceito em 24 de maio de 2024)

Research into pollination ecology provides information on plant reproduction, interactions with pollinators and biodiversity conservation. *Humiria balsamifera* occurs only in South America and presents an infraspecific complex with 10 varieties recorded in the most recent taxonomic revision. The current study aimed to evaluate the phenological events of flowering and fruiting, floral biology, floral visitors, and the reproductive system of *H. balsamifera* var. *floribunda*, in a restinga area in Maranhão, Brazil, in the year 2017. The production of floral buds, flowers, and fruits in 20 individuals was evaluated by the Fournier method. The phenophases presented no correlations with temperature, humidity, and rainfall, except for the production of immature fruits, which increased in the drier months. The species presents a large number of flowers in cymose-paniculate inflorescences, which open at 7:00 am and last less than a day. Nectar is the main resource exploited by the floral visitors. In all, 1393 floral visitors were observed distributed in 49 morphospecies, 94.75% of which were bees and wasps, including *Melipona subnitida*, *Apis mellifera*, *Xylocopa cearensis*, *Melipona fasciculata*, *Polybia sericea* and *Megalopta amoena* as the most abundant. Visitor activity occurred in all daytime hours and months of the year, but the abundance of specimens increased with flowering and reduced rainfall. Reproductive system tests indicated that *H. balsamifera* var. *floribunda* presents facultative xenogamy, requiring pollen vectors for its reproductive success. This work reinforces data on other varieties of the species and demonstrates the environmental importance of the plant to sustain fauna.
Keywords: nectar, restinga, floral visitors.

Pesquisas em ecologia da polinização fornecem informações sobre a reprodução das plantas, interações com polinizadores e conservação da biodiversidade. *Humiria balsamifera* ocorre apenas na América do Sul e apresenta um complexo infraespecífico com 10 variedades descritas na revisão taxonômica mais recente. O estudo teve como objetivo avaliar os eventos fenológicos de floração e frutificação, biologia floral, visitantes florais e sistema reprodutivo de *H. balsamifera* var. *floribunda*, em uma área de restinga no Maranhão, Brasil, durante 2017. A produção de botões florais, flores e frutos em 20 indivíduos foi avaliada pelo método de Fournier. As fenofases não apresentaram correlações com a temperatura, umidade e pluviosidade, com exceção da produção de frutos imaturos que aumentou nos meses mais secos. A espécie apresenta grande número de flores em inflorescências cimoso-paniculadas, que abrem a partir de 7:00h, e duram menos de um dia. O néctar é o principal recurso explorado pelos visitantes florais. Ao todo foram observados 1393 visitantes florais distribuídos em 49 morfo-espécies, sendo 94,75% de abelhas e vespas, entre elas *Melipona subnitida*, *Apis mellifera*, *Xylocopa cearensis*, *Melipona fasciculata*, *Polybia sericea* e *Megalopta amoena* como as mais abundantes. A atividade dos visitantes se estendeu por todo o dia e meses do ano, mas a abundância aumentou com a floração e redução das chuvas. A espécie foi caracterizada como xenogâmica facultativa, com a necessidade de vetores de pólen para seu sucesso reprodutivo. Este trabalho reforça dados sobre outras variedades de *H. balsamifera* e demonstra a importância ambiental da planta como mantenedora da fauna.
Palavras-chave: néctar, restinga, visitantes florais.

1. INTRODUCTION

The family Humiriaceae A. Juss. comprises eight genera, with 64 species distributed in the Neotropical region from Nicaragua to southern Brazil, and a single species that occurs distinctly in western Africa [1]. The genus *Humiria* comprises 5 species, including *Humiria balsamifera*

(Aubl.) A. St. Hil. found in the Guianas, Brazil, Colombia, Peru, Suriname, and Venezuela [1]. This species occurs in Brazil from the North region to the Southeast region, in the phytogeographic domains of Amazonia, Caatinga, Cerrado, and Atlantic Forest [2], especially in areas of white sand and rocky terrain [1].

The species *H. balsamifera* has medicinal potential with antimalarial [3], antimicrobial [4, 5], and anti-inflammatory [6] action due to the presence of a wide variety of terpenes [3] and flavonoids [5] in its leaves and stem bark, and the fruit of the species is rich in vitamin C and phenolic compounds [7]. The plant has economic and ecological importance, both for the use of its wood [8], and for its drupaceous fruits that serve as food for various birds, reptiles, and mammals, including humans [8]. In addition, its environmental value has been verified as a nesting substrate for stingless bees [9] and for honey production [10], due to the great abundance of inflorescences with nectariferous flowers.

Phenotypic plasticity is characteristic of *H. balsamifera*, with individuals ranging from shrub to tree, depending on the habitat where they occur [11]. A particularity of the species is its infraspecific complex, in which Cuatrecasas [12] distinguished 14 varieties and two forms, based on leaf and endocarp morphology. In his recent monograph of Humiriaceae, Prance [1] recognized the existence of only 10 varieties. The Amazon basin is home to the greatest wealth of varieties, the most common being *balsamifera* (typical variety), *guianensis*, and *floribunda* [1, 11]; in particular, the etymology of the latter is due to its abundance of flowers [13]. Although *H. balsamifera* var. *floribunda* (Mart.) Cuatr. can be found in woodlands, it generally occurs on white sandy soils mixed with some humus [11], such as woodlands and restinga. This variety is most widely dispersed in the Amazon, but occurs as far south as Rio de Janeiro [13].

Studies indicate that the *H. balsamifera* infraspecific complex exhibits substantial morphological overlap between vegetative and reproductive characters [14] and is probably interfertile [1], as found by Holanda et al. (2015) [15] who found no prezygotic barriers between two varieties. According to Cavalcante (2010) [11], *H. balsamifera* is a plant with a continuously flowering, and is visited by numerous floral visitors, however, these characteristics can change according to geographic location. Despite this, few studies considering pollination biology have been carried out with the species, highlighting the varieties *balsamifera* f. *attenuata* and *guianensis* in Roraima [15] and *parvifolia* in Bahia [16], although the latter has been re-established to the rank of species - *Humiria parvifolia* A. Juss. [1]. In both studies, *H. balsamifera* was considered to have melitophilia syndrome.

Pollination ecology studies encompass the interactions between flowers and their visitors [17], in order to understand mating rates, pollinator behavior and the maintenance of intraspecific gene flow [17, 18], as well as to provide support for appropriate management aimed at preserving native fauna and flora. The field of pollination ecology is broad and interdisciplinary, depending on floral biology, in which the manifestations of flower life and the various floral attributes are verified. The floral characteristics determine the pollination syndromes, which can be more specialized or generalist [19]. Around 87% of angiosperms depend on cross-pollination promoted by biotic vectors [20], with the predominance of bees [21, 22]. The dynamics of animal interaction are related to the plant's reproductive phenology [23], in which the phenophases are influenced by abiotic factors, such as variations in rainfall [22]. Particularly in restinga environments in the north-east of Brazil, flowering seems to increase in the dry season [24, 25], coinciding with the period of greatest bee activity [25].

On the eastern coast of Maranhão, the species *H. balsamifera* is well distributed in the restinga vegetation, with a predominance of shrubby habits [26], and contributes to the structure of the pollination network in the region by supplying nectar all year round [27]. Given the wide territorial distribution of the species and complexity of varieties, the aim of this study was to characterize the reproductive phenology, floral biology, reproductive system, and floral visitors of *H. balsamifera* var. *floribunda* in the Lençóis Maranhenses National Park, Brazil, thus contributing to increasing the knowledge about this species.

2. MATERIAL AND METHODS

2.1 Study area

The study was carried out in Barreirinhas, Maranhão, Brazil, within the area of the Lençóis Maranhenses National Park – PNLM (Figure 1). The region's climate is tropical megathermal, with a mean annual temperature of around 28.5°C, mean relative humidity of 79%, and mean annual rainfall of 1800 mm, with rainfall concentrated from January to June and the driest months from July to December [28]. The PNLM has an area of 155,000 ha, and the vegetation occupies 453.28 km^2, of which 89% is characterized as the restinga type, and 10.2% and 4% as mangroves and riparian forests, respectively [29].

In the study area, shrubby restinga vegetation predominates. This type of vegetation in PNLM is adapted to soils with low humidity and nutrient availability, and some of the main plant species are *H. balsamifera* and *Byrsonima* sp. Rich. ex Kunth [26]. The presence of only the variety *H. balsamifera* var. *floribunda* has been confirmed by researchers at the National Institute for Amazonian Research (INPA). In the region, the species has a predominantly shrubby habit, with a few individuals of medium tree size.

In the locality, some research has shown that different plant species provide floral resources for floral visitors, such as *Anacardium occidentale* L., *Borreria verticillata* (L.) G. Mey., *Byrsonima* sp., *Chamaecrista ramosa* (Vogel) H.S. Irwin & Barneby, *Chrysobalanus icaco* L., *Coccoloba* spp., *Comolia lythrarioides* Naudin, *Doliocarpus* sp., *H. balsamifera*, *Mimosa misera* Benth., *Myrcia* sp., *Ouratea* sp., *Protium heptaphyllum* (Aubl.) Marchand, *Mouriri guianensis* Aubl., and others [10, 27].

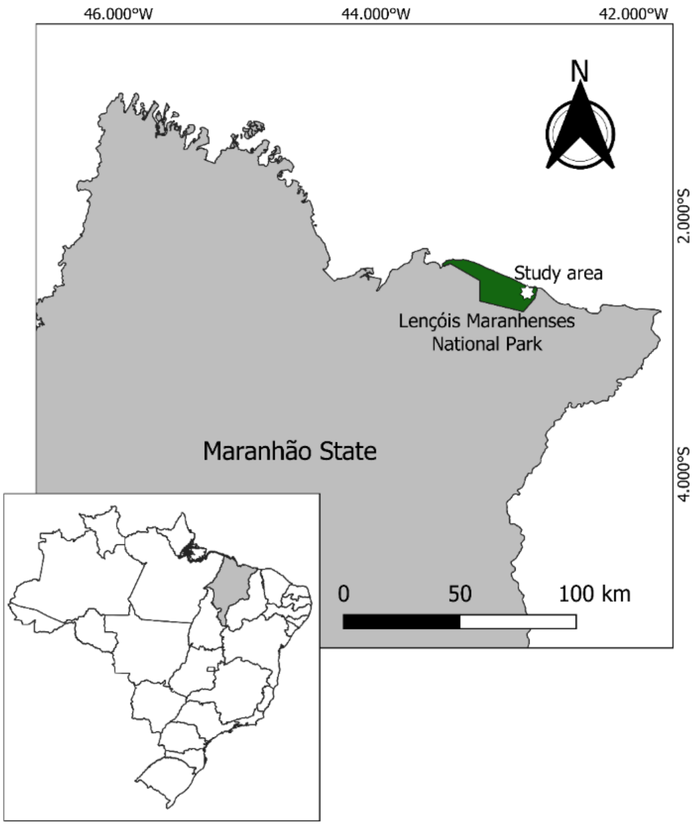

Figure 1. Location of the study area in the Lençóis Maranhenses National Park (highlighted in green), in Maranhão state, Brazil.

2.2 Data collection

Data collection was performed monthly from January to December 2017. The phenological analysis of the plant occurred in 20 randomly selected individuals, with a minimum distance of 20 meters between them, in an area equivalent to approximately 1,5 hectares. The phenophases observed were bud emission, flowers, immature fruits, and mature fruits. The percentages of intensity of each phenophase were considered according to the methodology of Fournier [30], in which a semi-quantitative interval scale is estimated in five categories (0 to 4), with a 25% interval between them: 0 = absence of phenophase; 1 = 1% to 25%; 2 = 26% to 50%; 3 = 51% to 75%; 4 = 76% to 100%. Thus, for each month the following formula was calculated: %Fournier = Σphenophase x 100 / N x 4, where Σphenophase corresponded to the sum of phenological intensities of all individuals and N to the total number of individuals (N = 20).

The main characteristics of floral biology were observed, as described in this paragraph. The number of flowers was quantified in 60 inflorescences, and the average number of flowers opened per day was verified in 20 inflorescences. The type of floral reward to visitors was defined through direct observation. Floral buds isolated with voile tissue (n = 40) served to track the onset, sequence, and duration of anthesis, and stigmatic receptivity was tested with 0.25% potassium permanganate ($KMnO_4$) solution [17]. Pollen grain viability was performed with 2% acetic carmine immediately after dehiscence of 10 flowers [17]. Subjective evaluation of odor production was carried out by olfactory characterization after keeping the flowers closed in a glass container for 20 minutes, at three times of the day: beginning of anthesis, midday and late afternoon. The odor also was perceived in the environment during the activity time. Nectar volume was measured after anthesis from isolated flowers in pre-anthesis (n = 20) with a 2μl microcapillary pipette [15, 31] and sugar concentration in nectar was calculated using a Milwaukee portable refractometer (scale from 0% to 85% Brix). Morphometric data was measured with a digital caliper (n = 20 flowers): style length (mm), large stamen length (mm) and small stamen length (mm) [15]. Pollen grains had their dimensions obtained under an optical microscope (n = 20): polar and equatorial diameters.

The reproductive system was tested using buds in pre-anthesis of 10 specimens. After performing the following procedures, the buds were isolated with voile tissue: 1. Agamospermy or apomixis (seed formation without sexual fusion between gametes) – buds had their styles cut (n = 40); 2. Autogamy (spontaneous self-pollination) – buds were only isolated (n = 977); 3. Induced self-pollination (manual self-pollination) – pollen was transferred to the stigma of the flower itself (n = 120); 4. Geitonogamy (cross-pollination) – stigma received pollen from a flower of another inflorescence, but from the same individual (n = 80); 5. Xenogamy (cross-pollination) – stigma received pollen from a flower of a different individual (n = 84); 6. Natural pollination (control) – In this case buds were marked and kept exposed to the environment (n = 868). All tests were followed until fruit formation or not. The "self-incompatibility index" (ISI) was obtained by dividing the percentage of fruit resulting from self-pollination by the percentage of fruit formed by xenogamy [32]. The "reproductive efficiency" (RE) was obtained by dividing the percentage of naturally pollinated fruits by the percentage of xenogamous fruits [33].

Monthly, floral visitors were observed and collected from morning twilight until nightfall, between 5:00 am and 6:00 pm, for 40 minutes/hour (12 days in a year x 560 minutes per day = 6,720 minutes total or 112 hours). Specimens with floral visitors were observed for a maximum of 20 minutes/hour. The behavior was evaluated in relation to the way of approaching the flower and the activity of collecting resources, thus defining categories: 1. Effective pollinators (EP) – those able to touch the sexual organs with high frequency; 2. Occasional pollinators (OP) – those able to touch the anthers and stigmatic surface, but observed with low frequency in the flowers; 3. Robbers/thieves (RT) – visitors who remove the resource without touching the anthers and stigma [34]. The insects were collected using an entomological net after visits to the flowers, sacrificed with ethyl acetate, and placed in labeled vials. Individuals from different orders of insects were identified by experts. The specimens are deposited in the entomological collection of the Laboratório de Estudos sobre Abelhas (UFMA). Authorization for capture of wild animals *in situ*: SISBIO – nº. 55992-1; authorization code – 79655811.

The temperature and relative humidity of the air in the region were obtained automatically every half hour with a datalogger (Icel - HT 4000). Rainfall was obtained from the National Institute of Meteorology - INMET Chapadinha station (No. 82.382) [35].

2.2 Data analysis

The relationship of reproductive phenophases (buds, flowers, immature fruits, and mature fruits) with climatic factors (temperature, relative humidity, and precipitation) was analyzed by Spearman's correlation (p = 0.05) [36]. A simple linear regression was used to compare the richness and abundance of floral visitors with flowering intensity and rainfall (p = 0.05). The analyzes were carried out with the software XLSTAT version 2020.3.1.

3. RESULTS

The population of *H. balsamifera* var. *floribunda* showed simultaneous production of buds, flowers, and fruits. Floral buds and flowers occurred in all months of 2017, with a peak in June for both phenophases. Fruiting was also seen throughout the analyzed period, but the peak of immature fruits occurred in August and the peak of mature fruits in September (Figure 2A). Correlation analysis indicated only significance of immature fruit production with temperature (r_s = 0.59), humidity (r_s = -0.81), and rainfall (r_s = -0.71). The other phenophases were not correlated with any climatic variable ($p > 0.05$) (Table 1). Climatic data for the region are presented in Figure 2B.

Table 1. Spearman's correlation between reproductive phenophases of Humiria balsamifera *var.* floribunda *and climatic data in 2017 in Lençóis Maranhenses National Park, Brazil.*

Phenophases	Temperature	Relative Humidity	Rainfall
Floral bud	0.028	-0.134	-0.254
Flower	0.000	-0.169	-0.332
Immature fruit	0.649*	-0.881*	-0.884*
Mature fruit	0.495	-0.435	-0.233

* Significance level with $p < 0.05$

The flowers of *H. balsamifera* var. *floribunda* are hermaphrodite, white, pentamerous, actinomorphic, and small (~5mm), with approximately 22 to 134 floral buds (average 57.46 ± 23.21) gathered in axillary or subterminal cymose-paniculate inflorescences. The sexual organs are exposed, the androecium has 20 erect stamens united alternately into 10 majors and 10 minors, and the gynoecium has a 5-lobed capitate stigma. The flowers have anthers and stigma proportionally at the same height (homostylia) = Large stamen (4.35 mm ± 0.25), Small stamen (3.76 mm ± 0.30) and, Style (2.81 ± 0.28).

The flowers do not have a pattern of opening in the inflorescence but can occur anywhere, interspersed with developing floral buds. The daily availability of flowers is two to 11 flowers/inflorescence/day. Floral anthesis starts slowly from 7:00 am, with some flowers only showing total petal separation at around 10:00 am.

From the beginning of anthesis, the stigma is receptive, and pollen is available to floral visitors (homogamy). The pollen grains are yellow, monad, tricolporate, medium-sized (Polar view – 38.15 µm ± 3.77; Equatorial view – 40.45 µm ± 3.50), with high pollen viability (96.8%). About 8h after anthesis, the anthers begin to detach, the stigma loses receptivity, and in the late afternoon, the petals begin to detach easily, and the flower lasts less than a day. The withered stamens, ovary, and calyx remain until the next day, when fertilization takes place; in some flowers the petals fall off completely only on the following day.

The sweetish odor released by the flowers was observed from the time of anthesis until the end of the day, functioning as a long-distance attractant. The flowers have a nectariferous disk surrounding the base of the ovary, with a low volume of nectar available 0.35 mL ± 0.03 and brix concentration of 28.80% ± 2.58. Nectar supply is constant, but production declines over time. Although pollen is easily accessible, it is reduced per flower, and the main resource collected by floral visitors is nectar.

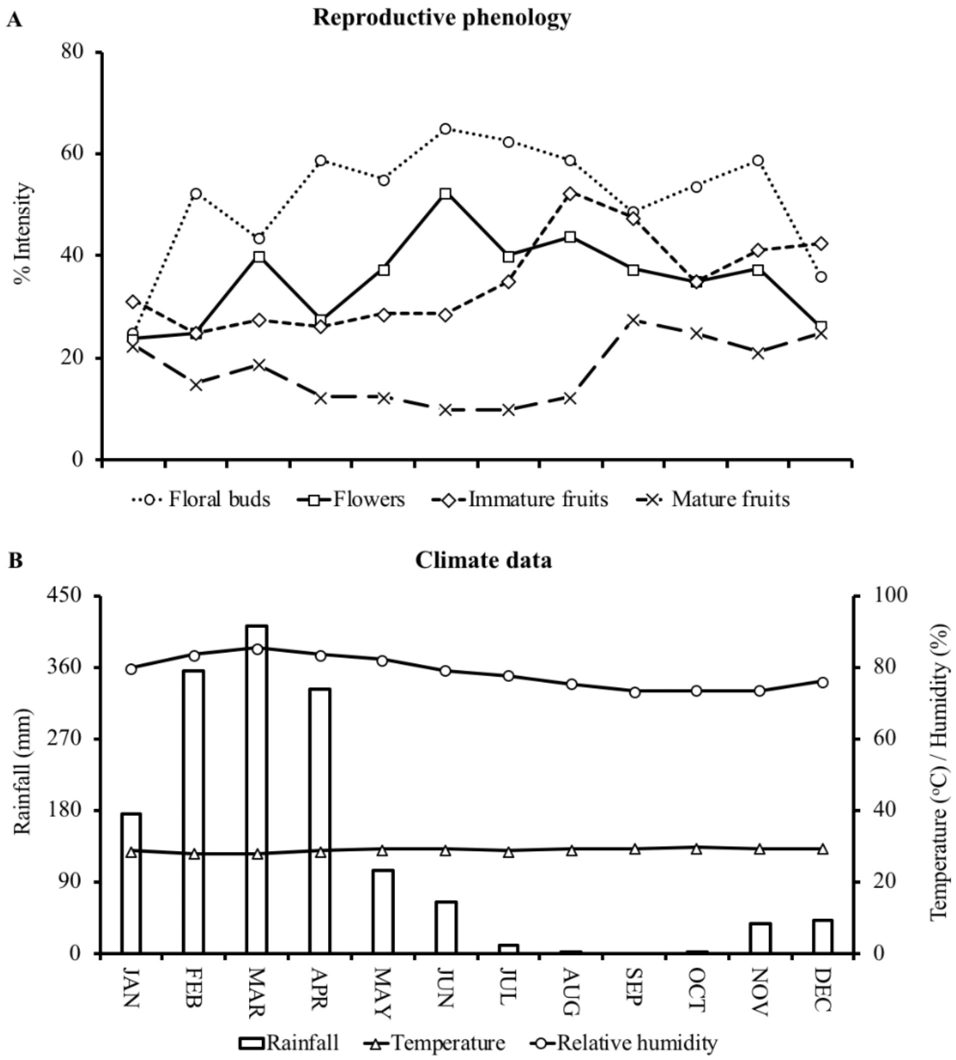

Figure 2. Reproductive phenology of Humiria balsamifera *var.* floribunda *and climate data in 2017, in Lençóis Maranhenses National Park, Brazil. A. Percentage index of intensity for floral buds, flowers, immature fruits, and mature fruits. B. Rainfall, mean temperature, and mean relative humidity.*

The results of the reproductive system tests are presented in Table 2. *Humiria balsamifera* var. *floribunda* did not show reproduction by apomixis, that is, without the presence of pollen grains. In the spontaneous self-pollination and manual self-pollination tests reduced fruit production occurred (<1%), which was slightly higher in the geitonogamy experiment, with self-pollination between flowers of different inflorescences (10%).

The highest fruiting success occurred in cross-pollination between different individuals, with 52.4% fruit formation. The calculation of the self-incompatibility index was 0.23, lower than the minimum self-incompatibility (0.25) [32]. The rates obtained by crossing between individuals and by fruit formation by self-pollination indicate that the variety is facultative xenogamous, requiring external agents (pollinators). Considering the percentage of fruit formation by control and cross-pollination, the reproductive efficiency index was 0.244, a relatively low value for natural pollinator efficiency.

Table 2. Fruit production by the reproductive system tests of Humiria balsamifera *var.* floribunda.

Tests	Flowers	Fruits formed	Frequency (%)
Agamospermy	40	0	0
Spontaneous autogamy	977	1	0.1
Induce autogamy	120	1	0.8
Geitonogamy	80	8	10.0
Xenogamy	84	44	52.4
Natural pollination (control)	868	111	12.8

The flowers of *H. balsamifera* var. *floribunda* were visits by 49 species (morphotypes), with a total of 1383 individuals, of which 89% were bees, 6.44% wasps, 2.46% diptera, 1.37% butterflies, 0.29% beetles, 0.22% ants, and 0.22% hummingbirds (Table 3). The months of July and April had the highest number of species recorded, 26 and 24, respectively, while from August to November only 9 species occurred (Figure 3). The bees *Melipona (Melipona) subnitida* (37.24%), *Apis mellifera* (26.54%), *Xylocopa (Neoxylocopa) cearensis* (9.54%), and *Melipona (Melikerria) fasciculata* (7.66%) had the highest frequency of visits and were the only visitors recorded in all the 12 months (Figure 4).

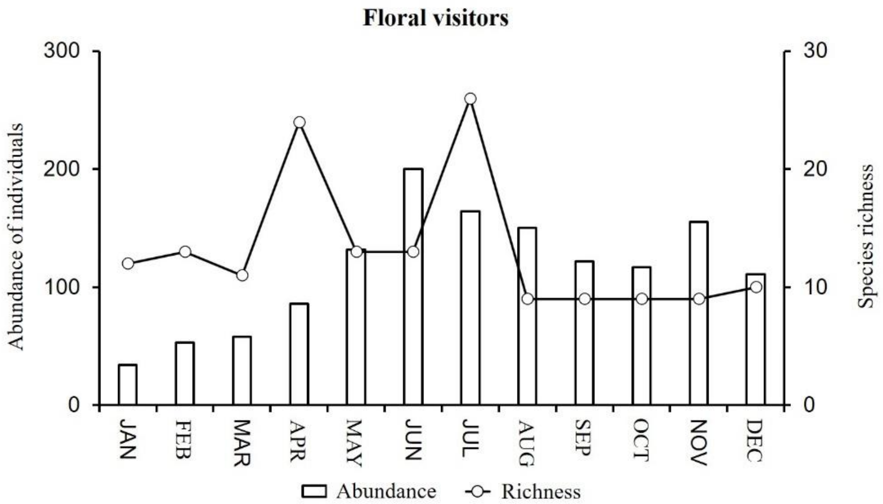

Figure 3. Abundance of individuals and richness species on visits to the flowers of Humiria balsamifera *var.* floribunda*, in 2017, in Lençóis Maranhenses National Park, Brazil.*

The floral visitor guilds did not show distinct behavior, with Hymenoptera, Diptera, and Lepidoptera recorded at any time of day (Table 3). In particular, the bees *Megalopta amoena* and *Xylocopa cearensis* were recorded in the crepuscular hours, but the former was observed foraging only in low light incidence and for a restricted period of no more than 30 minutes. Nectar was the resource sought by the floral visitors, as it is easily accessible regardless of the length of the mouth apparatus of the insects.

Three species were considered effective pollinators, 29 occasional pollinators, and 17 robbers/thieves. The bee species were considered the main effective pollinators of the plant because they frequently touched the reproductive organs of the flower and moved among the individuals. They landed directly on the flower, introducing the glossa between the stamens, groping the nectary in search of nectar, and by doing so, pollen grains became adhered to their head, ventral part, and/or leg, especially in the morning and early afternoon when pollen grains were more abundant on the anthers. In particular, the social bee species stayed longer exploring the inflorescences of the same individual.

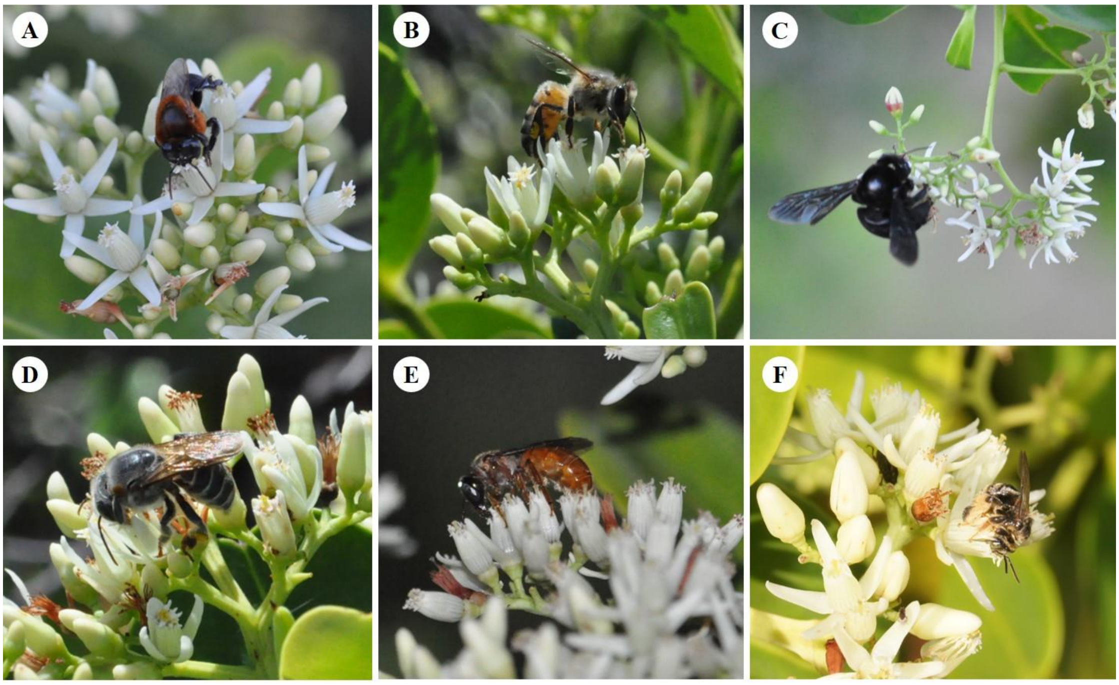

Figure 4. Flower-visiting bees of Humiria balsamifera *var.* floribunda*, in the Lençóis Maranhenses National Park, Brazil. A.* Melipona subnitida. *B.* Apis mellifera. *C.* Xylocopa cearensis. *D.* Melipona fasciculata. *E.* Megalopta amoena. *F.* Exomalopsis analis.

Bees were also considered the main occasional pollinators, followed by Lepidoptera. Butterflies were seen occasionally on the flowers and moved quickly between individuals. Some diptera and wasp representatives stayed longer on inflorescences than bees. Seven morphotypes of diptera were recorded only from January to July, the only exception was Bombyliidae sp.1 which also occurred in October. There were also some records of Ants, Coleoptera, and Apodiformes in the flowers of *H. balsamifera* (Table 3).

Linear regression analysis showed that the richness of floral visitors in each month had no correlation with flowering and rainfall (Figures 5A and 5B), but the number of visitors recorded was lower in the rainy season and increased with flowering (Figures 5C and 5D).

Table 3. Floral visitors of Humiria balsamifera *var.* floribunda *in a shrubland restinga area, Maranhão, Brazil. Months: January to June = rainy season; July to December = dry season; Activity hours: 5h to 18h; Function: EP – Effective pollinator, OP – Occasional pollinator, RT – Robbers/thieves.*

Species	Total	Months	Hours	Function
Hymenoptera: Bees (17)				
Apis mellifera Linnaeus, 1758	367	12 (Jan-Dec)	6h-18h	EP
Augochlora sp.	1	1 (Dec)	9h	OP
Augochloropsis sp.	1	1 (Jun)	10h	OP
Centris (*Centris*) *caxiensis* Ducke, 1907	17	5 (May/Jul-Oct)	6h-11h/13h	OP
Centris (*Centris*) *decolorata* Lepeletier, 1841	1	1 (Jul)	8h	OP
Centris (*Centris*) *flavifrons* (Fabricius, 1775)	2	2 (Apr/Jun)	8h	OP
Centris (*Melacentris*) *rhodoprocta* Moure & Seabra, 1960	1	1 (Sep)	14h	OP
Ceratina (*Crewella*) sp.	7	4 (Jan-Feb/Jul/Dec)	7h/9h/13h	OP
Dialictus sp.	3	1 (Jul)	15h-16h	RT
Exomalopsis (*Exomalopsis*) *analis* Spinola, 1853	14	2 (Jun-Jul)	7h/14h-17h	OP
Megalopta amoena (Spinola, 1853)	45	9 (Apr-Dec)	5h/17h-18h	RT

Melipona (*Melikerria*) *fasciculata* Smith, 1854	106	12 (Jan-Dec)	8h-17h	EP
Melipona (*Melipona*) *subnitida* Ducke, 1910	515	12 (Jan-Dec)	6h-17h	EP
Pseudaugochlora pandora (Smith, 1853)	3	2 (May/Jul)	9h-10h/15h	OP
Trigonopedia sp.	1	1 (Jul)	7h	OP
Xylocopa (*Neoxylocopa*) *cearensis* Ducke, 1910	132	12 (Jan-Dec)	5h-18h	OP
Xylocopa (*Neoxylocopa*) *grisescens* Lepeletier, 1841	15	8 (Jan-May/Jul-Aug/Dec)	5h/7h-8h/10h/12h-14h/16h-18h	OP
Hymenoptera: Wasps (11)				
Pepsis decorata Perty, 1833	6	5 (Jan-Apr/Jun)	6h/10h-12h/14h-15h	OP
Pepsis sp.2	4	4 (Apr/Jun-Jul/Dec)	8h/11h/17h	OP
Polistes canadensis (Linnaeus, 1758)	1	1 (Apr)	15h	RT
Polistes carnifex (Fabricius, 1775)	2	1 (Apr)	15h	RT
Polybia (*Myrapetra*) sp.2	5	3 (Feb-Apr)	10h/14h/16h	OP
Polybia sericea (Olivier, 1792)	59	9 (Mar-Nov)	6h-17h	OP
Synoeca surinama (Linnaeus, 1767)	2	2 (Apr/Jul)	8h/12h	OP
Thynnidae sp.	3	2 (Nov-Dec)	9h-10h	RT
Zethus mexicanus (Linnaeus, 1767)	2	2 (Feb/Jul)	14h-15h	RT
Morphotype sp.02	3	2 (Jan/Nov)	9h/12h-13h	RT
Morphotype sp.03	2	2 (Jan/Sep)	9h/14h	RT
Hymenoptera: Ants (1)				
Cephalotes sp.	3	2 (Jan/Apr)	9h/15h	RT
Diptera (8)				
Bombyliidae sp.1	3	2 (Jul/Oct)	11h-13h	RT
Bombyliidae sp.2	6	1 (Jul)	10h-13h	RT
Chrysomya sp.	1	1 (Jul)	14h	RT
Copestylum sp.	1	1 (May)	7h	RT
Palpada sp.1	6	5 (Jan-Apr/Jul)	7h/9h/13h/17h	OP
Palpada sp.2	13	5 (Mar-Jul)	7h-13h/16h	OP
Sarcophagidae sp.	2	1 (Apr)	11h/15h	RT
Tabanidae sp.	2	2 (Apr-May)	7h/10h	RT
Lepidoptera (10)				
Aphrissa sp.	1	1 (Feb)	12h	OP
Ascia monuste (Linnaeus, 1764)	1	1 (Jul)	12h	OP
Calycopis sp.	2	1 (Apr)	13h/16h	OP
Heraclides sp.	1	1 (Oct)	13h	OP
Hesperiidae sp.1	2	1 (Aug)	11h	OP
Hesperiidae sp.2	1	1 (Jul)	18h	RT
Pseudolycaena marsyas (Linnaeus, 1758)	3	2 (Jul/Nov)	7h-8h/11h	OP
Morphotype sp.03	5	2 (Apr-May)	7h/10h/18h	OP
Morphotype sp.04	2	2 (Apr/Jul)	18h	OP
Morphotype sp.05	1	1 (Jun)	10h	OP
Coleoptera (1)				
Chrysomelidae sp.	4	3 (Jan-Feb/Apr)	6h/8h-9h/14h	RT
Apodiformes (1)				
Trochilidae sp.	3	3 (Feb-Apr)	14h/16h	OP

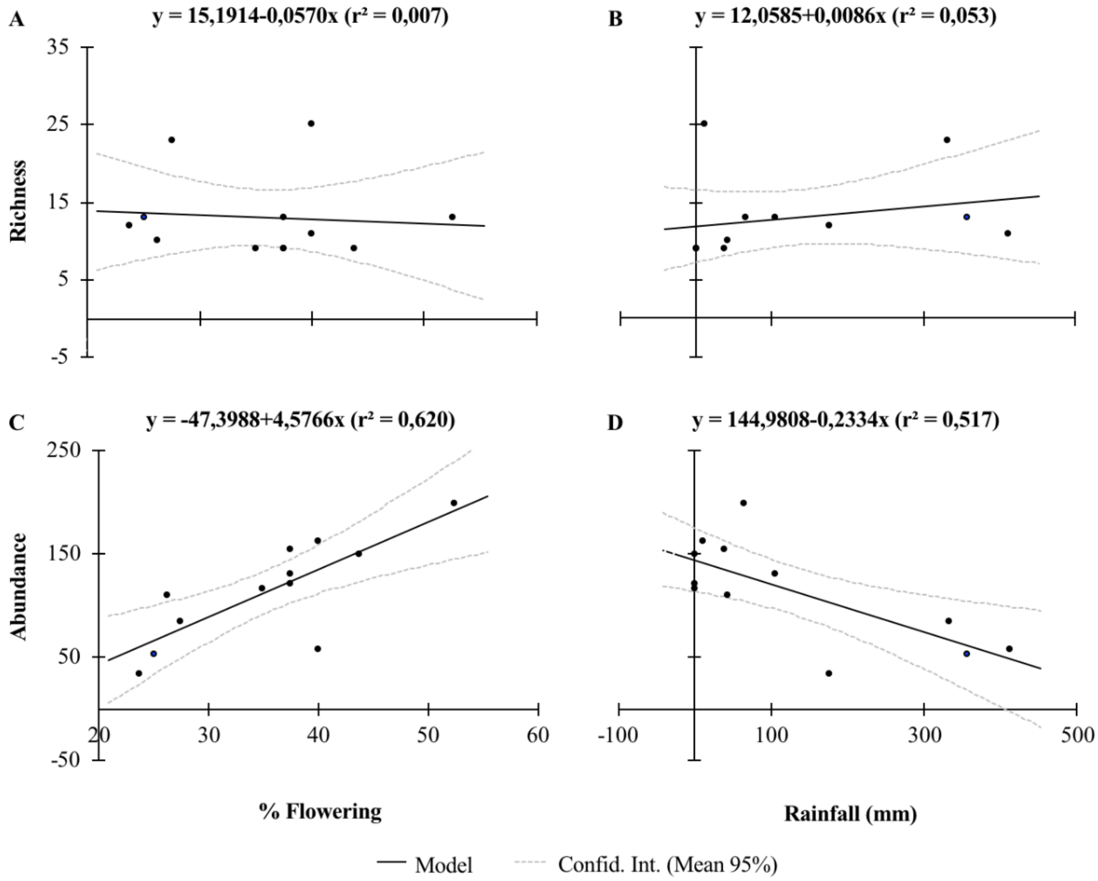

Figure 5. Simple linear regression analysis of the richness and abundance of floral visitor species of Humiria balsamifera *var.* floribunda *in relation to flowering intensity and rainfall recorded in 2017. A. Species richness x flowering. B. Species richness x Rainfall. C. Number of visitors x Flowering. D. Number of visitors x Rainfall.*

4. DISCUSSION

The reproductive phenophases of *H. balsamifera* var. *floribunda* in the restinga of the Lençóis Maranhenses National Park are continuous throughout the year, with flowering peaking in June and fruiting between August and September, thus presenting a continuous pattern [37]. In restinga environments, where the vegetation is on sandy soils and undergoes coastal influence, extensive flowering of plant species is relatively common [24].

Although cyclic patterns of phenology are expected with environmental seasonality, only immature fruit production was correlated with abiotic factors. Increased fruit production in the dry season may be favored by decreased rainfall, which reduces damage to fruit formation [38]. A relative increase in bud/flower production was also observed in the transition period from the rainy to the dry season, and maintenance of the highest bloom in the drier months. A clue to the prolonged and even increased flowering of this species in the dry period may be due to its shrub life habit with sufficient biomass to store water [39], the shallow water table in the restinga of the study region, and the increase in temperature and photoperiod in the period [40, 41], or adaptation to the behavior of floral visitors [42], especially bees, with increases in the number of individuals in the flowers in the dry period, as recorded by Pinto et al. (2022) [27]. In a restinga environment, the reproductive period of plant species increases in the dry season [24, 25]. In the study region, *Mauritia flexuosa* L. has been found to increase flowering and fruiting in the dry season, in order to favor germination in the rainy season [28]. A study conducted in the Pantanal with a continuous flowering species (*Prosopis rubriflora* Hassl.) indicated higher flowering and fruiting in the dry season [40].

The flowering of *H. balsamifera* is continuous, but apparently the peaks can vary from one location to another, something common for many tropical plants [37]. In the Amazon region it is most pronounced between the months of May and September, and fruiting occurs thereafter, with many ripe fruits in November [11, 15], and in Bahia, the flowering peaks were seen between November and May [24]. It is possible that in a region the intensity of flowering in the population may demonstrate some variation from one year to the next [10].

One characteristic of the individuals of *H. balsamifera* var. *floribunda* was the high synchrony of the phenophases, with practically all showing flower and fruit production in the period, something verified previously in the species [15, 43]. However, despite this, we found that the individual flowering intensity in each month was highly heterogeneous. This pattern of flowering among individuals is common in the tropics [44], and this may be due to differences in the microhabitat of each specimen. The non-correlation of the bud/flower phenophases with environmental factors may be explained by this heterogeneity among individuals.

The floral biology of *H. balsamifera* var. *floribunda* did not show expressive differences regarding the time of anthesis and stigma receptivity, and pollen and nectar availability compared to other varieties studied, such as var. *balsamifera* f. *attenuata* and var. *guianensis* [15] and var. *parvifolia* [16], the latter currently considered *H. parvifolia* [1]. The observation of available nectar from the moment of flower anthesis is important for floral visitors, who can carry already viable pollen to a receptive stigma of another flower. This nectar, although in small quantities, is easily accessible and continuously offered by the flowers, ensuring that visitors seek the largest number of flowers throughout the day [45, 46].

The reproductive system tests indicated that the *floribunda* variety is facultative xenogamous, with low fruit formation by self-pollination, and higher by cross-pollination. This result resembles the varieties *balsamifera* f. *attenuata* and var. *guianensis* [15], and differs in part from that observed by Costa and Ramalho (2001) [16] who determined the variety *parvifolia* (now *H. parvifolia*) as obligate xenogamous. However, we tested the geitonogamy of the plant for the first time, and the results indicated that this species can slightly form fruits by crossing flowers of the same individual. This frequency of geitonogamy can be attributed to the behavior of flower visitors foraging for a long time on the flowers of the same individual.

The closeness in the percentage obtained in the control (12.8%) and geitonogamy tests (10%) is an indication that many fruits are formed by crossing within the same individual. Under natural conditions few fruits were formed when compared to the number of flowers produced, estimated at up to 50 thousand per plant [24]. This condition may be related to the amount of pollen that reaches the stigma of a compatible flower, the period of stigmatic receptivity, natural abortion of young flowers and fruits, and the presence of plunderers [47, 48]. We consider it very unlikely that the low percentage of fruits formed under natural conditions is due to the low efficiency of pollinators, although the result indicates this.

Among the floral visitors, bees and wasps accounted for more than 95% of the total, similar to the results seen in other varieties [15, 16]. These Hymenoptera were the main pollinators because they frequently touched the reproductive structures of the flower and moved among the individuals. In fact, the floral attributes of *H. balsamifera*, such as diurnal anthesis, white coloration, production of nectar in small quantities and with very good quality in dissolved sugars (~30%), and emission of a mild and pleasant odor, indicate the species as presenting a melitophilia syndrome [19, 49]. However, we think that the species presents a more generalist pollination, because the plant receives a great wealth of visitors seeking nectar in morphologically unrestricted flowers.

The species is characterized by abundant inflorescences, which function as a "visual display" and maximize floral attractions such as color, odor, and resources. The gradual opening of flowers on the inflorescences over days causes its individuals to have an extended flowering period for several weeks, and this continuous flowering may be a reproductive strategy to ensure the attraction of a large number of potential pollinators [47, 50]. In our study the richness of floral visitors (49 spp.) was almost 3x higher than found for the species in another coastal region (17 spp.) [16] and in the Amazon (18 spp.) [15].

Eusocial bees (*M. subnitida, M. fasciculata, A. mellifera*) were abundant visitors to the plant, a result similar to that verified by Holanda et al. (2015) [15]. Because the activity of these species occurs practically throughout the observation period, it demonstrates their adaptability to the local climatic conditions of high temperatures and strong winds, and also the importance of *H. balsamifera* as a continuous source of nectar. In an interaction network study that analyzed the pollen present on the bodies of social bees that visit *H. balsamifera* in the locality, it was found that many individuals carry pollen specific to the plant, which favors pollination [27]. The body size of these bees and foraging movements propitiate touching the fertile structures of the flower, but due to the behavior of floral fidelity and prolonged foraging on a plant, eusocial bees can facilitate the self-pollination of monocline flowers [51], which would explain the 10% of geitonogamy.

An evolutionary conflict is the so-called "plant dilemma", where an increase in the number of flowers would attract more pollinators, but at the same time expand the number of visits on flowers of the same plant during the same pollinator foraging route, causing high rates of geitonogamy [52]. Since in this study eusocial bees were very important, we can assume that, as suggested by Ramalho (2004) [51], this plant takes advantage of the activity of these bees to facilitate its partial self-incompatibility condition (facultatively inbreeding), but this cost may be low for the plant, since the pollinator has limited activity capacity on each trip, and thus they can visit other plants of the same species during the foraging event [52]. Furthermore, the high number of floral visitors may reduce the availability of nectar, forcing them to increase the foraging area, and thus, promote a greater number of visits between plants, favoring cross-pollination.

Xylocopa cearensis was the third most frequent bee species in this study and is well documented as visiting *H. balsamifera* in the restinga habitats of Northeast Brazil [16, 49]. In these coastal environments, where the vegetation is relatively open and at low altitude, there is a predominance of pollination by large and medium-sized bees [53, 54]. Despite being abundant in the plant's flowers, we consider that the species acts only as an occasional pollinator, as it frequently visited other plant species during the same foraging route, which is a problem because it can transfer nonspecific pollen from another plant to the stigma of *H. balsamifera*.

The orders Hymenoptera, Diptera, and Lepidoptera presented high species richness, but overall, low abundance each. This may occur due to the lower fidelity of many of these insects to the plant, occasionally seeking nectar to feed, and also due to the low population density of the species, or even the influence of external factors, such as rainfall, temperature, and wind [55].

After bees, wasps were the morphotypes that most visited the flowers at any time of the day and month of the year, especially the social species *Polybia sericea*. Wasps are considered robust insects that tolerate wide variations in light and temperature [55]. In the current study several species were observed visiting the plant, but in the Amazon only the species *Brachygastra bilineolata* was reported [15].

Although it is considered that Diptera do not have a restricted period of activity during the year [50], with the exception of Bombyliidae sp.1, we observed greater diversity of this group in the flowers of *H. balsamifera* in the rainy months and transition to the dry season, which may be associated with the preference of these insects for wetter environments [47]. 75% of the Diptera morphospecies were considered thieves, as they collected nectar without displaying the appropriate behavior to pollination, such as touching all the reproductive structures of the flower and moving between the flowers. In general, this type of interaction is negative for plants. However, a positive aspect may be that the theft of the floral resource results in a decrease in the supply of a flowering individual, which forces pollinators to move to another plant and cross-pollinate [56].

Butterflies were considered occasional pollinators, since they contacted the fertile structures of the flower, but their visits were infrequent. These insects commonly visited a few flowers per individual and flew to another plant in the surroundings, a fundamental behavior to maintain gene flow between subpopulations of *H. balsamifera*, even more so when considering that these insects maintain constancy in foraging over long distances [57, 58].

The occurrence of hummingbirds was very low, and they visited the flowers quickly, moving through different individuals. In the campo rupestre in Bahia, *H. balsamifera* was considered an important resource for these birds [59].

5. CONCLUSION

The continuous flowering pattern of *H. balsamifera* var. *floribunda* encourages the maintenance of a rich biodiversity of floral visitors, and its prolonged fruiting can feed several fruit-eating animals. The increase in these phenophases in drier periods may be beneficial for the sustenance of the community, in case of food shortage from other plants.

The species presents flowers that fit the melitophilia syndrome, but despite the absolute dominance of bees, it receives different guilds of floral visitors in search of its easily accessible nectar. This interaction of *H. balsamifera* with many insects can characterize the species as having generalist pollination, and this should be a key factor for its reproductive success, since its facultative xenogamous condition it needs pollen vectors to maintain its gene variability.

H. balsamifera var. *floribunda* in the restinga of Lençóis Maranhenses National Park does not show significant differences in its floral biology in relation to other varieties in different localities and biomes. Further studies with the species are needed to better understand the trends of phenological phases in different years, because observation of only 12 months is a clear limit for long-term data interpretation.

6. ACKNOWLEDGMENTS

This work received financial support from the Fundação de Amparo à Pesquisa e ao Desenvolvimento Científico e Tecnológico do Maranhão - FAPEMA (number 01171/17); and from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES (Finance Code - 001).

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