

Original Articles

Pollination and reproductive biology of *Byrsonima pachyphylla* and *B. verbascifolia* (Malpighiaceae)

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Abstract

The reproductive biology of *Byrsonima pachyphylla* and *B. verbascifolia* in the Brazilian state of Tocantins in the Cerrado biome (Savanna) is described unprecedentedly in this work. This genus belongs to the Malpighiaceae family, which is one of the main sources of resources for bees. Inflorescences of each species were collected for analysis of morphometry and other floral characteristics at Fazenda São Judas Tadeu (10° 48' 31" S and 48° 26' 52" W), located in the municipality of Porto Nacional, Tocantins, Brazil. Floral visitors were observed directly in the field during the peak flowering period. The analysis of the reproductive system was carried out through manual cross-pollination, manual self-pollination, spontaneous self-pollination, apomixis, and natural pollination (control group). The floral characteristics are related to the melittophily syndrome. The bees *Centris aenea*, *C. fuscata*, *C. sponsa*, and *C. vittata*, were the effective pollinators. *Trigona spinipes*, *Xylocopa frontalis*, *X. suspecta*, *Epicharis flava*, *Augochlora mendax* and *Apis mellifera* performed occasional and sternotribic pollination. Reproductive tests of *B. pachyphylla* showed fruiting success of 40% by manual cross-pollination and 53% by natural pollination (control group), while through spontaneous self-pollination, manual self-pollination and apomixis there was no reproductive success. For *B. verbascifolia*, 33% of fruits formed by spontaneous self-pollination, 43% by manual self-pollination, 60% by manual cross-pollination and 63% in the control group, while by apomixis there was no reproductive success. *B. pachyphylla* is self-compatible and *B. verbascifolia* is self-incompatible and they both depend on pollinators to ensure their reproductive success.

Keywords: floral biology, sympatric species, reproduction, bees, Cerrado.

Introduction

In Brazil, this family has approximately 300 species, belonging to 32 genera (Barroso et al., 1991). For the genus *Byrsonima* Rich., at least 150 species are found in the country (Cronquist, 1981) in various plant formations, including in the Cerrado (savanna) biome (Neri et al. 2007, Miranda Absy 1997). *B. pachyphylla* A. Juss. and *B. verbascifolia* (L.) DC are objects of the present study and are both commonly called murici. They are species native to Brazil and have life forms that vary between bushes and trees (Mamede & Francener, 2015).

The genus *Byrsonima* belongs to the Malpighiaceae family, which represents one of the main sources of resources for bees (Vogel, 1990). A striking feature of most Malpighiaceae species present in Brazil is the fact of having flowers that contain an abundant composition of lipids instead of nectar (Rezende & Fraga, 2003). Their flower oils have up to 4 times more energy than nectar carbohydrates (Buchmann, 1987).

The main floral resources of the Neotropical Malpighiaceae consist of oil and pollen, which are collected by several groups of bees from the Centridini (Anderson, 1979), Tapinotaspidini and Tetrapedini (Neff & Simpson, 1981) tribes. The collection of oil happens during the visit of the bees to the flowers through the friction of the basitarsal combs located on their anterior and median legs. These animals can break the cuticle of the elaiophores, oil-accumulating structures of Malpighiaceae flowers. Soon thereafter, they transfer the oil to the scopae, located on the tibiae of the hind legs, together with the pollen grains that adhered to the ventral part of their body during the visit to the flower (Sazima & Sazima, 1989; Sazan et al., 2014).

Bees use floral oils to build and waterproof their nests (Neff & Simpson, 1981; Buchmann, 1987; Vinson et al., 1997). During oil collection, they can additionally carry pollen. The mixture of these two resources serves as food for bee larvae (Vogel 1974; Simpson & Neff, 1981), as well as for the nutrition of adult bees (Buchmann, 1987). The flowers of the *Byrsonima* species are organized in inflorescences of the simple terminal raceme type, having five unguiculate petals with yellow or auburn color. The flowers also have a modified petal that acts as a guide for possible pollinators, called a standard, characterized by the greater thickness of the claw in comparison with other petals (Costa et al., 2006).

The relationship between Malpighiaceae and their oil-collecting bees has mutually adapted over time through strong evolutionary interaction, leading to the production of oil by plants and the use and collection of this floral resource by guilds of bees to assure the reproductive success of these plants through the pollination process (Anderson, 1979; Buchman, 1987; Vogel, 1990).

The most recent studies of the *Byrsonima* genus show its potential for the food (De Barros et al., 2022; Costa et al., 2019, Stafussa et al., 2021) and pharmaceutical industries (Saldanha et al., 2016). Other studies highlight the pollination system of species of the genus: *B. guilleminiana* A. Juss., *B. crassa* Nied., *B. laxiflora* Griseb., *B. subterranea* Brade & Markgr. (Barros, 1992), *B. sericea* DC. (Teixeira & Machado, 2000; Costa et al., 2006; Rosa & Ramalho, 2007), *B. coccolobifolia* Kunth. (Benezar & Pessoni, 2006), *B. gardnerana* A. Juss. (Bezerra et al., 2009), *B. rotunda* Griseb., *B. umbellata* Mart. ex. A. Juss. (Mendes et al., 2011) *Peixotoa tomentosa* A. Juss. and *Byrsonima intermedia* A. Juss. (Carvalho-Leite et al., 2025). However, there are few studies of *B. pachyphylla* A. Juss. and *B. verbascifolia* (L.) DC. Works on plant floral biology for the state of Tocantins are still scarce, and this work represents an important contribution to the understanding of the reproductive strategies of plants in this biome and their associated pollinator guilds.

Therefore, this study presents for the first time the reproductive strategies and clarifies aspects of the ecology and pollination of *B. pachyphylla* and *B. verbascifolia* in an area of the Cerrado biome in the state of Tocantins, Brazil.

Methods

Study area. The study was carried out in two populations of *B. pachyphylla* and *B. verbascifolia* (approximately 1.5 km apart) in an area of Cerrado *stricto sensu*, at Fazenda São Judas Tadeu, located in the municipality of Porto Nacional, Tocantins, close to Highway TO 070, which connects Porto Nacional to the city of Brejinho de Nazaré (10° 48' 31" S and 48° 26' 52" W). The soil in this area is of the Red-Yellow Latosol type, with the presence of rocky fragments (Lima, 2000). According to the National Institute of Meteorology (INMET, 2015), the average annual rainfall in the last nine years was approximately 1,800 mm, concentrated between November and April.

Samples of botanical materials of *B. pachyphylla* and *B. verbascifolia* were deposited in the Tocantins Herbarium (HTO) of Federal University of Tocantins, under registration numbers 10,947 and 10,948.

Floral morphology. Fifteen inflorescences of each species were collected for analysis of morphometry and other floral characteristics. After collection, the inflorescences were stored in 70% alcohol until analysis in the laboratory. Thirty intact flowers, chosen at random, were used to carry out the following measurements: inflorescence length (rachis), number of buds and flowers per inflorescence, length and diameter of floral pedicels, and length and width of petals and elaiophores. All measurements were made using a digital caliper.

Anthesis. Floral anthesis was monitored in the field with 30 flowers of each species, duly marked and numbered, with the duration, time and opening sequence being recorded. To determine the period of stigmatic receptivity, manual cross-pollination tests were performed on 30 flowers of each species, 10 newly opened and 10 each 24 and 48 hours after opening (Dafni et al., 2005). After pollination, the flowers were isolated using tulle bags and monitored to verify the occurrence of fruit formation.

Pollination ecology. Floral visitors were observed directly in the field during the peak flowering period (June to October for *B. pachyphylla* and September to November for *B. verbascifolia*). Observations were carried out on 10 focal plants for 30 minutes for each plant, in the morning and afternoon, to record the time, duration and frequency of visits, as well as the visitors' behavior during these visits. These behaviors were classified into three categories: effective pollinator; occasional pollinator and resource plunderer (Inouye, 1980). Visiting insects were collected with the aid of a net and a killing chamber for later identification and analysis of the collected material. In the latter case, the visualization of the collected resources (oil and pollen) was performed with a stereoscopic microscope.

Reproductive system. To determine the reproductive system, five individuals were randomly sampled of each species. In each individual, six inflorescences (with buds in pre-anthesis) were marked with threads of different colors, which were isolated with tulle bags to avoid contact with possible pollinators. The flowers of each inflorescence were submitted to one of the following treatments: manual cross-pollination (the bud was emasculated and pollination was carried out by rubbing the anthers of a newly opened flower from another individual over the receiving stigmas); manual self-pollination (after opening, the stigmas received pollen from the anthers of the flower itself with the aid of a brush); spontaneous self-pollination (the inflorescences remained isolated until the formation of the fruit); and apomixis (the anthers were eliminated immediately after the flower opened, before dehiscence). Non-isolated inflorescences were used to evaluate the efficiency of natural pollination (control). Thirty repetitions were performed for each type of treatment. All marked inflorescences were monitored until fruit formation or not.

Results

The two species have similar floral morphology (Table 1, Figure 1), with yellow, hermaphrodite, pentamerous, zygomorphic flowers, with a differentiated petal (standard) and ten elaiophores, two in

each of the five sepals. Both species have an androecium consisting of ten stamens with introrse anthers of longitudinal dehiscence, while the gynoecium is composed of five stigmas. However, the inflorescences differ greatly regarding the number of flower buds and the length of the floral rachis. *Byrsonima verbascifolia* has much higher values than *B. pachyphylla* for these two traits.

The anthesis of both species occurred either synchronously (all petals opening at the same time) or sequentially (one petal opening at a time), starting at 6:00 am. At 7:00 a.m., all the flowers were open. In addition to the morning period, the flowers of *B. verbascifolia* also opened in the late afternoon between 4:00 and 5:00 pm. In both

Table 1. Characteristics of inflorescences and dimensions of flowers, elaiophores and petals (mean \pm standard deviation) of *Byrsonima pachyphylla* and *Byrsonima verbascifolia*.

Floral structures	<i>B. pachyphylla</i>	<i>B. verbascifolia</i>
Inflorescence		
Flower buds per inflorescence	17.80 \pm 5.52	24.76 \pm 3.25
Open flowers/inflorescence/day	6.36 \pm 3.11	6.43 \pm 2.81
Rachis length (mm)	34.55 \pm 18.49	143.34 \pm 17.08
Flower		
Pedicle length (mm)	9.10 \pm 1.18	11.18 \pm 1.48
Pedicle diameter (mm)	1.11 \pm 0.18	0.95 \pm 0.18
Elaiophores		
Length (mm)	3.34 \pm 0.38	3.48 \pm 0.23
Width (mm)	1.70 \pm 0.29	1.51 \pm 0.14
Petal – Claw		
Length (mm)	2.77 \pm 0.44	3.83 \pm 0.36
Width (mm)	0.53 \pm 0.10	0.51 \pm 0.10
Petal- Claw (standard)		
Length (mm)	3.07 \pm 0.52	4.31 \pm 0.46
Width (mm)	0.75 \pm 0.13	1.01 \pm 0.12
Petal – Limb		
Length (mm)	5.36 \pm 0.68	6.56 \pm 1.04
Width (mm)	5.86 \pm 0.73	7.11 \pm 1.04
Petal- Limb (standard)		
Length (mm)	4.53 \pm 0.61	5.18 \pm 0.55
Width (mm)	4.80 \pm 0.71	5.84 \pm 0.75

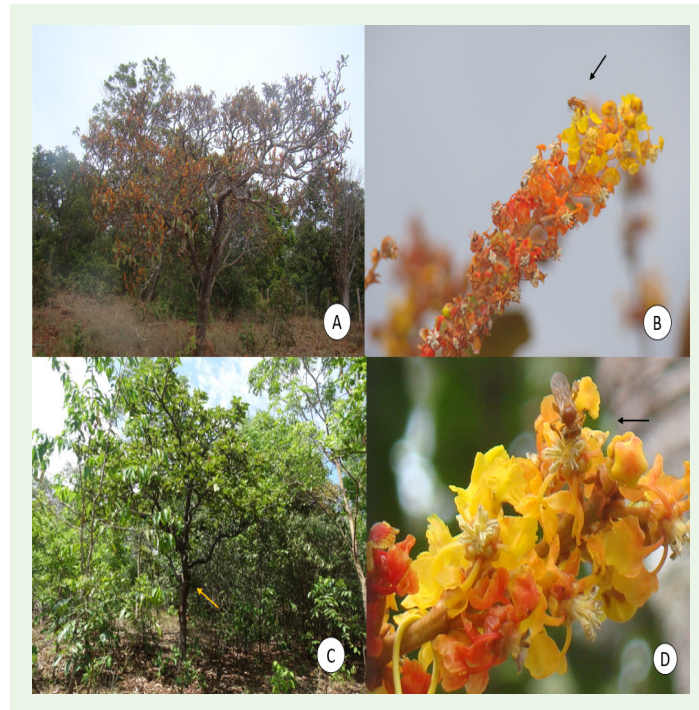


Figure 1. A) *Byrsonima pachyphylla* in bloom; B) Pollination of inflorescences of *B. pachyphylla* by *Centris aenea*; C) *Byrsonima verbascifolia* adult; D) Flower of *B. verbascifolia* receiving a visit from *C. aenea*; in an area of Cerrado *stricto sensu*, Porto Nacional, Tocantins, Brazil.

species, anthesis began with the slow distension of the petal limbs, at which time the anthers began to dehisce. The stigma was only receptive during the first day of anthesis. From 6:00 a.m. or 4:00 p.m. on the second day, the flowers began to close. The duration of anthesis was therefore approximately 24 hours. Soon thereafter, a process of changing the corolla occurred, which became completely withered and brownish in color, and then the petals began to fall.

Many species of bees visited the flowers of *B. pachyphylla* and *B. verbascifolia* (Tables 2 and 3); among them *Centris aenea*, *C. fuscata*, *C. sponsa*, *C. vittata*, *Trigona spinipes*, *Xylocopa frontalis*, *X. suspecta*, *Epicharis flava*, *Augochlora mendax* and *Apis mellifera*. Visits were recorded mainly in the morning (Figures 1 and 2).

Centris aenea, *C. fuscata* and *C. sponsa* bees were observed visiting both *Byrsonima* species, while *C. vittata* was recorded only in *B. verbascifolia*. All *Centris* species were considered effective pollinators. They also collected both oil and pollen grains. These bees positioned themselves on the flower in order to touch the stigmas and anthers with the abdominal region of their body, characterizing sternotribic pollination. During the visits, these bees exhibited vibrating movements with their bodies to press the anthers and promote the release of pollen grains. Subsequently, they scraped the pollen grains from their bodies using their median legs and deposited

them in the scopae, located on the hind legs (according to Vogel, 1974). To collect oil, the bees attached themselves to the standard petal using their mandibles and, with the aid of the basitarsal combs present on the first two pairs of legs, scraped the elaiophores and subsequently transferred this resource to the scopae.

Trigona spinipes specimens were observed visiting the two species studied by perching on the flower to collect pollen. However, due to their small size, they were only occasionally able to touch the abdominal region in the reproductive structures and carry out pollination. Often their visits resulted only in looting of resources, being denominated as pillagers.

Xylocopa frontalis was recorded visiting both *Byrsonima* species, while *X. suspecta* was seen only on *B. verbascifolia*. These bees maintained the behavior of landing on the flower and collecting pollen through vibratory movements touching the reproductive structures to effect sternotribic pollination. However, due to their low visitation rates, they were considered occasional pollinators.

Epicharis flava bees were recorded collecting pollen and oil from both species. During the visit, they landed on the flower and performed sternotribic pollination. The collection of floral resources was carried out through their vibratory behavior. After collection, they cleaned the body with the help of the front and middle legs,

Table 2. Floral visitors of *Byrsonima pachyphylla* in an area of Cerrado *stricto sensu*, Porto Nacional, Brazil. F = Frequent (> 35%), LF = Less Frequent (16 – 36%), R = Rare (6 – 15%), VR = Very Rare (< 5%); O = Oil; Po = Pollen; EP = Effective Pollinator, P = Pillager; OP = Occasional Pollinator.

Floral visitors	Total visits	%	Frequency	Resource(s) collected	Duration of visits (seconds)	Pollination efficiency
<i>Centris aenea</i>	67	60.36	F	O/Po	6	EP
<i>Centris fuscata</i>	8	7.20	R	O/Po	8	EP
<i>Centris sponsa</i>	8	7.10	R	O/Po	8	EP
<i>Trigona spinipes</i>	9	8.10	R	Po	15	OP/P
<i>Xylocopa frontalis</i>	7	6.30	R	Po	9	OP/P
<i>Epicharis flava</i>	3	2.70	VR	O/Po	7	OP
<i>Augochlora mendax</i>	4	3.60	VR	Po	13	OP
<i>Apis mellifera</i>	5	4.50	VR	Po	12	OP

Table 3. Floral visitors of *Byrsonima verbascifolia* in an area of Cerrado *stricto sensu*, Porto Nacional, Brazil. F = Frequent (> 35%), LF = Less Frequent (16 – 36%), R = Rare (6 – 15%), VR = Very Rare (< 5%); O = Oil; Po = Pollen; EP = Effective Pollinator, P = Pillager; OP = Occasional Pollinator.

Floral visitors	Total visits	%	Frequency	Resource(s) collected	Duration of visits (seconds)	Pollination efficiency
<i>Centris aenea</i>	49	54.44	F	O/Po	6	EP
<i>Centris fuscata</i>	2	2.22	R	O/Po	8	EP
<i>Centris sponsa</i>	9	10.0	R	O/Po	8	EP
<i>Centris vittata</i>	11	12.22	R	O/Po	9	EP
<i>Trigona spinipes</i>	8	8.88	R	Po	12	OP/P
<i>Xylocopa frontalis</i>	5	5.55	VR	Po	9	OP
<i>Xylocopa suspecta</i>	2	2.22	VR	Po	7	OP
<i>Epicharis flava</i>	2	2.22	VR	O/Po	8	OP
<i>Apis mellifera</i>	2	2.22	VR	Po	11	OP

and transferred the resources to the hind legs where the scopae are located. Due to the low frequency of visits, these bees were considered occasional pollinators.

Augochlora mendax was recorded performing pollen collection only on the species *B. pachyphylla*. These bees landed on the stamens, clamped their mandibles on the anthers and performed vibratory movements to promote the release of pollen grains, which were deposited throughout their body. Finally, they transferred the

pollen to the scopae. This bee species was considered an occasional pollinator due to its low frequency of visitation.

Apis mellifera bees performed only pollen collection from the two species. During their visits, they landed on the flower and occasionally actually touched the reproductive structures to carry out pollination, thus being considered an occasional pollinators.

Pollination tests showed different results of fruit formation. In *B. pachyphylla*, control pollination resulted in 53% success of fruit

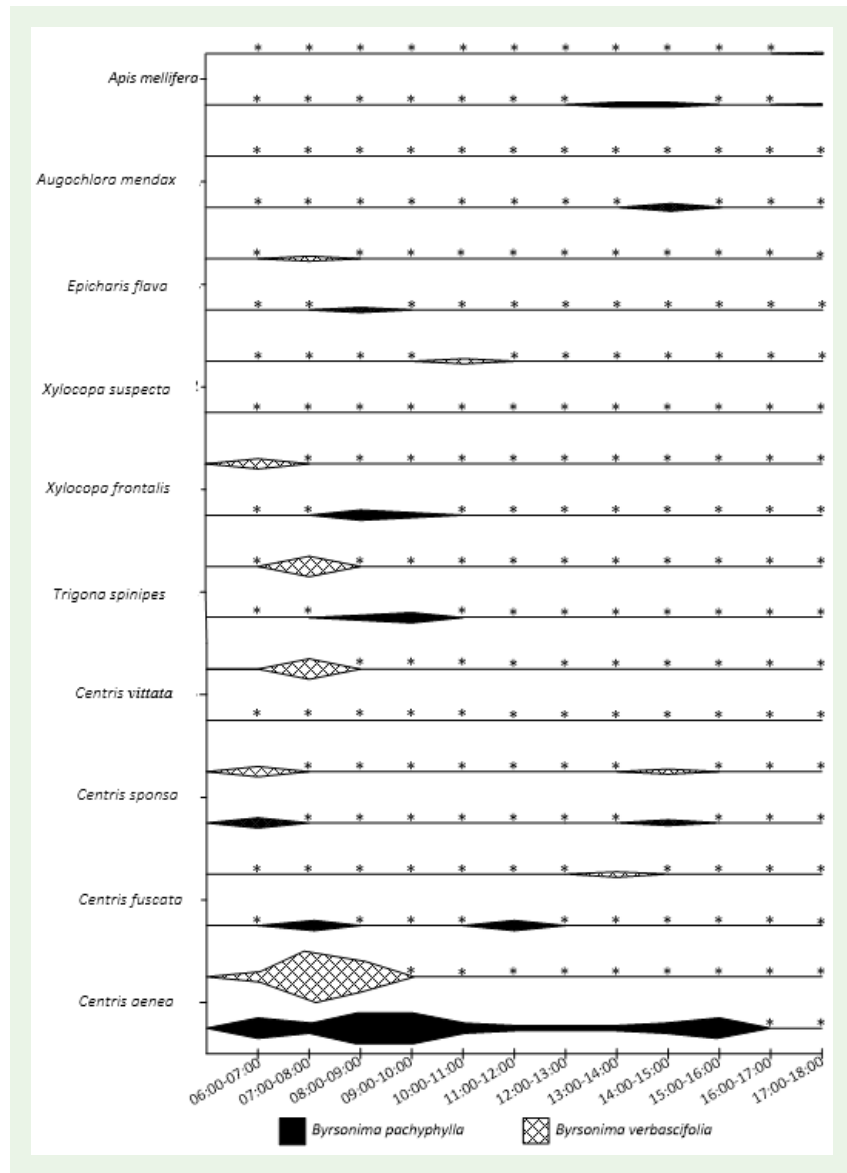


Figure 2. Number of visits by time class to flowers of *Byrsonima pachyphylla* and *Byrsonima verbascifolia* in an area of Cerrado *stricto sensu*, Porto Nacional, Brazil. *Indicates no visits.

production. In manual cross-pollination, reproductive success was 40%. For manual self-pollination, apomixis and natural spontaneous self-pollination, fruit production did not occur (Table 4). These results indicate that the species is self-incompatible. For the species *B. verbascifolia*, control pollination generated 63% success in fruit production. In manual cross-pollination, reproductive success was 60%, while in manual self-pollination and natural spontaneous self-pollination, reproductive efficiencies were 43% and 33%, respectively. In apomixis, no fruit production occurred (Table 5). Such results indicate that the species is self-compatible.

Discussion

Pollination by vibration of *Centris* spp. has also been recorded in other *Byrsonima* genera, such as *B. crassa* Nied., *B. laxiflora* Griseb., *B. subterranea* Brade & Markgr., (Barros, 1992), *B. sericea* DC. (Teixeira & Machado, 2000; Costa et al., 2006; Rosa & Ramalho, 2007), *B. coccolobifolia* Kunth. (Benezar & Pessoni, 2006), *B. gardnerana* A. Juss. (Bezerra et al., 2009) and *B. rotunda* Griseb., *B. umbellata* Mart. ex. A. Juss. (Mendes et al., 2011). *Centris* bees vibrate their bodies to facilitate the collection of oil located in the elaiophores of

Table 4. Characteristics of the reproductive system of *Byrsonima pachyphylla* in an area of Cerrado *stricto sensu*, Porto Nacional, Brazil.

Treatments	Flowers	Fruits	Success (%)
Apomixis	30	0	0
Spontaneous self-pollination	30	0	0
Manual self-pollination	30	0	0
Manual cross pollination	30	12	40
Control	30	16	53

Table 5. Characteristics of the reproductive system of *Byrsonima verbascifolia* in an area of Cerrado *stricto sensu*, Porto Nacional, Brazil.

Treatments	Flowers	Fruits	Success (%)
Apomixis	30	0	0
Spontaneous self-pollination	30	10	33
Manual self-pollination	30	13	43
Manual cross pollination	30	18	60
Control	30	19	63

Byrsonima flowers. These bees store the oil in the scopae of their hind legs, while pollen is carried throughout their bodies (including the scopae). These resources are used for their own nutrition and that of their larvae, and also for the maintenance of their nests (Vogel, 1974; Rêgo & Albuquerque, 1889).

The floral characteristics of the studied species are related to the melitophily syndrome, which is common in *Byrsonima* (Anderson, 1979; Faegri & Van Der Pijl, 1979). The differentiation observed in the standard petal is considered to act as a guide for the landing and positioning of floral visitors. The greater thickness of the claw on this petal is related to its role in supporting these insects during their visits to flowers (Anderson, 1979; Sazima & Sazima, 1989; Vogel, 1990; Teixeira & Machado, 2000; Sigrist & Sazima, 2004; Costa et al., 2006; Mendes et al., 2011; Boas et al., 2013). The bees use this thicker and reinforced claw to secure their jaws and thus support themselves on the flower when vibrating to collect the oil (Anderson, 1979; Sigrist & Sazima, 2004).

The number of flower buds per inflorescence and the number of open flowers per inflorescence per day reported by other authors varies greatly between the two *Byrsonima* species. *B. gardnerana* obtained an average of 1.7 open flowers per inflorescence per day, while *B. sericea* had 10.6 flowers (Costa et al., 2006). Totals of 10.4 flower buds/inflorescence were registered in *B. umbellata* and 29 in *B. rotunda* (Mendes et al., 2011). The variation found in our study in relation to flower buds is in line with the previous findings for these species.

The sequence of anthesis observed in the flowers was consistent with that reported for other species of the genus *Byrsonima* (Barros, 1992; Teixeira & Machado, 2000; Benezar & Pessoni, 2006; Costa et al., 2006; Rêgo & Albuquerque, 2006; Mendes et al., 2011; Boas et al., 2013). Variations in corolla color likely serve as visual cues to floral visitors, indicating the end of anthesis and the consequent depletion of floral resources such as pollen and oil. Nonetheless, the retention of these senescent flowers on the plants appears to contribute to maintaining the visual prominence of the inflorescences, thereby enhancing their attractiveness to potential visitors over greater distances (Rêgo & Albuquerque, 1989; Costa et al., 2006).

The floral visitors of *B. pachyphylla* and *B. verbascifolia* recorded in the present study were similar to those found for several species of this genus (Rêgo & Albuquerque, 2006; Mendes et al., 2011; Boas et al., 2013; Sazan, 2014). The effectiveness of pollinators is classified according to their total contribution to the reproductive success of a given plant species. Therefore, this can be measured through pollinator effectiveness and visitation intensity (Freitas, 2013). *Centris* spp. were considered the most effective pollinators of the studied species, mainly due to the high pollination efficiency and the high visitation rates when compared to the other pollinators. The interaction between these bees and Malpighiaceae flowers developed through co-evolution, which is characterized by morphological and functional adaptations that occur in both groups (Vogel, 1990; Simpson & Neff, 1981, 1983; Machado, 2004). In addition, *Centris* bees have been considered in several studies to be the main pollinators of the neotropical Malpighiaceae (Rêgo & Albuquerque, 1989; Teixeira & Machado, 2000; Carvalho et al., 2005; Benezar & Pessoni, 2006; Rêgo & Albuquerque, 2006; Mendes et al., 2011; Boas et al., 2013; Sazan, 2014).

The frequency of visits, mainly in the morning, was common in *Byrsonima* (Boas et al., 2013; Rêgo & Albuquerque, 2006; Mendes et al., 2011; Sazan, 2014). During this period, most of the flowers of the two species investigated in the present study were at the beginning of their anthesis process, which could have been advantageous for the bees due to the greater availability of resources. The collection of pollen by vibration registered in *Centris* spp., *Epicharis* sp. and *Augochlora* sp. is common in Malpighiaceae flowers (Barros,

1992; Sazima & Sazima, 1989; Teixeira & Machado, 2000; Sigrist & Sazima, 2004; Benezar & Pessoni, 2006; Costa et al., 2006; Rêgo & Albuquerque, 2006; Mendes et al., 2011; Boas et al., 2013; Sazan, 2014) and presents the advantage of the speed of each visit, which can increase the number of visits per time interval. This type of collection is typical in flowers with non-poricidal dehiscence (Rêgo & Albuquerque, 1989), as is the case of the studied species.

The occasional pollinator behavior of *Trigona* sp. was also recorded in a study of *B. crassifolia* (Rêgo & Albuquerque, 1989) and in another study involving *B. umbellata* and *B. rotunda* (Mendes et al., 2011). The oil collected by these bees contributes to the adhesion of pollen to their body surface (Rêgo & Albuquerque, 1989), which helps transport a greater amount of pollen grains to the nest. *Apis mellifera* has also been recorded in a remnant area of Cerrado in the Midwest region of Brazil by carrying out visits to *B. pachyphylla* (Boas et al., 2013). Although this bee is exotic and often competes for resources with native pollinators, the species is a good pollinator and has a great ability to forage in a wide range of plant species. This is due to its great ability to explore and adapt to different environments with different characteristics (Köppler et al., 2007).

In spontaneous self-pollination, manual self-pollination, cross-pollination and apomixis treatments, the low number of fruits formed is considered common in Malpighiaceae (Barros, 1992; Costa et al., 2006; Mendes et al., 2011; Boas et al., 2013; Sazan, 2014). This may be related to the presence of a stigmatic cuticle that makes it difficult for pollen to adhere to the stigma (Sigrist & Sazima, 2004). *B. pachyphylla*, being a self-incompatible species, depends on pollinating agents to ensure its reproductive success. This characteristic was evident when comparing the number of fruits formed by this species (28 fruits) with those produced by *B. verbascifolia* (60 fruits), the latter species being classified as self-compatible. Similar results were found for *B. gardnerana* (Costa et al., 2006) and *B. sericea* (Dunley, 2009). Although *B. verbascifolia*

is a self-compatible species, the success of reproductive tests demonstrated the importance of pollinators to ensure greater fruit production.

Conclusions

Based on the information presented in this study, it can be concluded that *Byrsonima pachyphylla* exhibits a self-incompatible breeding system, whereas *B. verbascifolia* is self-compatible. These sympatric *Byrsonima* species depend on the activity of *Centris aenea*, *C. fuscata*, and *C. sponsa*, which function as their effective pollinators and perform pollination through the vibration mechanism. Bees of the genus *Centris* were the ones that made the highest number of visits, indicating that their maintenance in the study area is fundamental to guarantee the flow of pollen between individuals of *Byrsonima* from different and even distant populations, thus contributing to increase the population genetic variability and fruit production by cross-pollination.

Author contributions

Andressa Cavalcante Meireles wrote the paper obtained and discussed the analysis, experimental, and estimated data. Ageu da Silva Monteiro Freire, Robério de Oliveira, Thalline Rodrigues da Silva, Wagner de Melo Ferreira and Rodney Haulien Oliveira Viana supported the writing of the paper.

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