

Reproductive biology and pollination of two species of *Byrsonima* Kunth in a Cerrado fragment in Central Brazil

Biologia reprodutiva e polinização de duas espécies de Byrsonima Kunth num fragmento de Cerrado no Brasil Central

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Abstract

Malpighiaceae contains approximately 1250 species in 68 genera with a variety of life styles, this family is one of a group of nine families that have a highly specialized organ secreting oil called elaiophores. The study was conducted from August 2012 to September 2013, in a Cerrado fragment at the University of Rio Verde, State of Goiás, Brazil. The weather in the region is tropical seasonal and the rainy season occurs from October to March, and the dry season, from April to September. The flowers of *Byrsonima basiloba* A. Juss. and *Byrsonima intermedia* A. Juss. show diurnal anthesis. The stigma receptivity extends for up to three days after anthesis. The pollen is white and powdery, and the viability for *B. basiloba* pollen is 96.2%, while for *B. intermedia*, it is 92.9%. In the reproductive system treatments, *B. basiloba* had 28.9% fruit production in natural conditions and 3.4% in xenogamy. Conversely, *B. intermedia* had the highest fruit production for xenogamy (36.8%), followed by natural pollination (13.8%). The female bees of the genus *Epicharis* were the most likely bee genus to collect pollen and oil during the period observed. The bees of the genus *Augochloropsis* collected only pollen, and *Paratetrapedia aff. Testacea* collected oil in flower buds during the pre-anthesis phase.

Keywords: Malpighiaceae, murici, oil-producing flowers, floral biology, melittophily, Apidae bees.

Resumo

Malpighiaceae contem aproximadamente 1250 espécies e 68 gêneros com variadas formas de vida, esta família é uma das nove famílias quem possuem um órgão especializado na secreção de óleo, chamado elaióforo. O estudo foi conduzido de agosto de 2012 a setembro de 2013 em um fragmento de Cerrado na Universidade de Rio Verde, Estado de Goiás. O clima da região é tropical com estação chuvosa ocorrente entre outubro a março e a estação seca de abril a setembro. As flores de *Byrsonima basiloba* A. Juss. e *Byrsonima intermedia* A. Juss. apresentam antese diurna. A receptividade estigmática estende por mais de três dias após a antese. O pólen é branco e pulverulento, a viabilidade do pólen para *B. basiloba* é 96,2%, enquanto para *B. intermedia* é 92,9%. Nos tratamentos para o sistema reprodutivo *B. basiloba* apresentou 28,9% de produção de frutos em condições naturais e 3,4% para xenogamia. Já *B. intermedia* teve maior índice de produção por xenogamia, (36,8%), seguido de polinização natural (13,8%). As abelhas fêmeas do gênero *Epicharis* foram vistas com maior frequência em todos os horários de observação coletando pólen e óleo. Já as abelhas do gênero *Augochloropsis* foram observadas coletando apenas pólen, e *Paratetrapedia aff. Testacea* foi observada coletando óleo em botões na fase de pré-antese.

Palavras-chave: Malpighiaceae, murici, flores produtoras de óleo, biologia floral, melitofilia, abelhas Apidae.

INTRODUCTION

Malpighiaceae contains approximately 1250 species in 68 genera with a variety of life styles, from herbaceous plants to arboreal species and even lianas (Souza & Lorenzi, 2012). The genus *Byrsonima* has approximately 150 species (Stevens, 2001), 48 are endemic to Brazil and 47 occur in the Cerrado domain (Mamede, 2013).

Malpighiaceae Neotropical species are part of a group of nine families that have a highly

specialized organ secreting oil called elaiophores. Vogel (1974) separated the elaiophores into two morphological types in epithelial elaiophores, which occurs in Malpighiaceae, and elaiophores in trichomes. This differentiated floral resource is collected from Malpighiaceae flowers by bees females of Centridini tribes, Tapinotaspidini and Tetrapediini (Hymenoptera: Apidae). These bees collect the oil for food or their larvae and impermeable to build nests of cells (Buchmann, 1987; Vogel, 1974; Neff &

Simpson, 1981; Frankie et al, 1989 Sazima & Sazima., 1989; Vogel, 1990 ;Vinson et al., 1997; Ribeiro et al, 2008). The mutual movement between particular flowers producing oil collecting bees and leads Malpighiaceae species to be encompassed in the oil flower pollination syndrome (Buchmann, 1987; Vogel, 1986).

The predominance of bee pollination in Cerrado and in it is strata was described by (Martins & Batalha, 2007; Ishara & Maimoni-Rodella, 2011; Silva et al., 2012. According to (Silberbauer-Gottsberger & Gottsberger, 1988), the floral resources available in the Cerrado can be vital for bee populations. However in recent decades the Cerrado has lost much of its area for agricultural plantations. The action of pollinators in native vegetation is essential for the maintenance of biodiversity, contributing to genetic variability in sexed plants (Imperatriz-Fonseca, 2004).

This study aimed to characterize the floral biology, to determine the reproductive system type, understand the behavior of flower visitors and identify effective pollinators for two species of Malpighiaceae, *Byrsonima basiloba* A. Juss. and *Byrsonima intermedia* A. Juss., which are from the Cerrado.

MATERIALS AND METHODS

Study area and plant species

The study was conducted from August 2012 to September 2013, in a Cerrado remnant at the University of Rio Verde, State of Goiás, Brazil (17°47'05''S, 50°58'00''W) with an altitude of 778 meters. The area has approximately 40 hectares and comprises two vegetation types of Cerrado, Cerrado *sensu stricto* and Cerradão (Ribeiro & Walter, 2008). It is surrounded by an experimental crop matrix and university buildings (Figure 1).



Figure 1. The study area is delimited by the white line.

Figura 1. Área de estudo delimitada pela linha branca.

The weather in the region is tropical seasonal – Aw, according to Köppen (1948), and is characterized by two well-defined seasons. The rainy season occurs from October to March, and the dry season, from April to September. The average annual precipitation is 1,600 mm and the average temperature varies between 20°C and 25°C throughout the year (Inmet, 2013). The soil is classified as Red-Yellow Latosol (Oxisol) (Embrapa, 2006). The soil is deep and well-drained and

has low fertility, high aluminum toxicity and a texture that ranges from clay-like to clay-sandy (Batista & Mattos 2007).

B. basiloba is arboreal, 2 m to 6 m high and commonly known as “murici-de-ema” or “murici de folhas brancas”. This species is found only in the Cerrado domain and is restricted to the central-west and southeast regions of Brazil. *B. intermedia* is shrubby, 0.5–2.5 m high and known as “murici-

pequeno”. It has a broad phylogeographic distribution, being found in the Amazon Rain Forest, Atlantic Forest and Cerrado (Mamede, 2013).

Floral biology

Fresh flowers were collected for mensuration. The measurements were performed for 30 inflorescences (length and number of buds) and 30 flowers. The measures of both species were compared using the X^2 test at a significance level of 0.05%. The viability of the pollen grains was estimated by cytoplasm staining using the aceto carmine technique at 1.2% (Radford et al., 1974). Fifteen slides for each species were prepared and photographed into three different fields using an optical photomicroscope. The stigma receptivity was determined by adding hydrogen peroxide to the stigma and observing the presence or absence of bubbles under a stereomicroscope (Kearns & Inouye, 1993). The odor emission was verified by storing newly opened flowers in glass jars for 24 hours. The records on floral events such as the time of opening, longevity and modifications during anthesis were observed between 06 h and 18 h.

Reproductive system

The inflorescences were isolated with buds using organza bags. Then, the following treatments were performed: cross-pollination (xenogamy) with emasculation – using pollen from one newly open flower from a different individual distant over ten meters; geitonogamy with emasculation – pollen from a different flower from the same individual; manual self-pollination - pollen from the same flower; spontaneous self-pollination – the inflorescence was isolated; apomixis – the anthers were removed and the flowers were isolated; natural pollination (control) – the inflorescences were labeled without isolation and were exposed to the flower visitors to verify pollination in natural conditions. The crosses were performed every day as soon as the flowers opened. The organza bags were kept until flower senescence or fruit formation.

The index of self-incompatibility (ISI, sensu Bullock, 1985) and the reproductive efficacy (RE) was calculated. The first is the percentage of fruits formed from manually pollinated flowers divided by the percentage of cross-pollinated flowers (xenogamy), and the second is the percentage of fruits formed in natural conditions divided by the percentage of fruits formed by cross-pollination (xenogamy) (Sobrevila & Arroyo, 1982).

Pollination

The behavior of the flower visitors, the duration and time of visits and the flower resource used were recorded by field observations at different times of day, totaling 96 hours of sampling. The visitors were classified based on size: small (length < 12 mm) or medium-large (length \geq 12 mm) and pollination efficiency (effective pollinators (for those that directly touched the reproductive structures during resource collection), thieves (when the visitor did not touch the reproductive structure and/or harmed or destroyed the anthers and/or stigma) and occasional pollinators (those who occasionally touched the reproductive structures) (Vilhena & Augusto, 2007; Bezerra et al., 2009).

RESULTS

Floral biology

The *B. basiloba* floral axis is greater than *B. intermedia*, but with a smaller number of flowers (Table 1). This structure was the only one to have similar values for both species. In *B. intermedia*, it was not possible to obtain the sepal measurements because elaiophores the covered almost completely. Both species have five free sepals, which are greenish in *B. basiloba* and yellowish in *B. intermedia*. The corolla in both species has five free yellow petals, which are unguiculate and alternate with the sepals. One of the petals (*banner*) is thicker than the other. In *B. basiloba*, the banner petal is larger than the other petals, and *B. intermedia*, is smaller.

Tabela 1. Médias e desvio padrão das inflorescências e estruturas florais (mm) de *B. basiloba* e *B. intermedia* (Malpighiaceae) em um fragmento de Cerrado no Brasil Central.

Table 1. Means and standard deviations of the inflorescences and flower structures (mm) of *B. basiloba* and *B. intermedia* (Malpighiaceae) in a Cerrado fragment in Central Brazil.

Structure	<i>Byrsonima basiloba</i>	<i>Byrsonima intermedia</i>
Inflorescence length (cm)	14.73 ± 7.03	10.19 ± 2.09
Number of flowers	42.6 ± 12.61	52.93 ± 16.63
Flower diameter	19.60 ± 0.50	12.10 ± 1.97
Pedicel length	7.53 ± 0.26	5.44 ± 0.86
Elaioflore length	2.40 ± 0.55	2.38 ± 0.38
Sepal length	2.72 ± 0.24	-
Sepal width	2.07 ± 1.09	-
Petal length	7.98 ± 0.75	5.77 ± 0.82
Petal width	5.81 ± 1.09	3.27 ± 0.52
Banner length	9.59 ± 2.14	4.93 ± 0.53
Banner width	8.05 ± 1.03	3.44 ± 0.53
Stamen length	3.87 ± 0.51	3.50 ± 0.42
Anther length	2.59 ± 7.03	2.29 ± 0.29
Carpel length	5.00 ± 0.63	4.50 ± 0.38
Style-stigma length	3.33 ± 0.74	2.99 ± 0.32

The androecium has ten homodynamous and free stamens, which consist of ditheous anthers and longitudinal dehiscence. The anther color ranges from white to yellow, and this structure becomes dry after dehiscence, gradually turning brown because of the absence of pollen. The pollen is white and powdery with high viability of approximately 96.2% for *B. basiloba* and 92.9% for *B. intermedia*. The gynoecium is composed of a superior ovary, syncarpous, tricarpeal, trilobular, with one egg of axilar placentation; it has three long, terminal and free styles, which remain in the drupaceous fruit. The stigma remained receptive up to three days after anthesis. No odor was noticed in either of the two species. Comparing the morphometric measurements of both species, the results show no significant statistical difference.

The opening of the flowers of the two species is diurnal, flowers were observed opening until around 4:30 pm. Anthesis can last from one to two hours. Sunlight seems to be sufficient for the opening of *B. basiloba* flowers, which had an anthesis peak between 6:00 am and 7:00 am. *B. intermedia* flowers may need more luminosity or a higher

temperature because more flowers were observed to be open from 10:00 am to 4:00 pm. In addition, during the cloudy days, these flowers did not easily open. The opening of the petals occurred in two ways: synchronous, with all petals opening at the same time, and sequential, with one petal opening at a time. When the petals opened, the anthers were already dehiscent. The flowers remained open and visible for up to 72 hours. Afterwards, the petals entered senescence, which can be identified by the change in color from yellow to reddish for *B. basiloba* but without any apparent alteration for *B. intermedia*.

Reproductive system

There was no formation of fruits through apomixis in the studied species or through spontaneous self-pollination for *B. intermedia*. The lowest rate of fruit formation was observed for the geitonogamy treatment. For *B. basiloba*, natural pollination resulted in the highest percentage of fruit formation; however, the spontaneous and manual self-pollination also produced fruits. Conversely, *B. intermedia* had the highest success in the xenogamy treatment (manual cross-

pollination), followed by natural pollination (Table 2).

Tabela 2. Resultados do sistema reprodutivo, eficiência reprodutiva (RE) e o Índice de autoincompatibilidade (ISI) de *B. basiloba* e *B. intermedia* (Malpighiaceae) em um fragmento de Cerrado no Brasil Central.

Table 2. Results of the experiments reproductive system, reproductive efficiency (RE) and index of self-incompatibility (ISI) of *B. basiloba* and *B. intermedia* (Malpighiaceae) in Cerrado fragment in Central Brazil.

Treatment	<i>Byrsonima basiloba</i>			<i>Byrsonima intermedia</i>		
	Flowers (n)	Fruits (n)	Fruit formation (%)	Flowers (n)	Fruits (n)	Fruit formation (%)
Natural pollination (control)	145	42	28.9	254	35	13.8
Spontaneous self-pollination	159	5	3.1	264	0	0
Manual self-pollination	118	5	4.2	118	7	5.9
Geitonogamy	115	1	0.9	101	5	4.9
Xenogamy	119	4	3.4	87	32	36.8
Apomixis	165	0	0	113	0	0
RE			8.5			0.37
ISI			1.2			0.16

According to the values obtained for the reproductive systems, *B. basiloba* can be considered a self-compatible species that exhibits reproductive behavior really close to that of autogamous to mixed species. This characteristic most likely contributed to its more efficient reproduction. *B. intermedia* can be classified as a self-incompatible species and can be considered allogamous, requiring a pollinator to produce fruits.

Pollination

During the observation period, six species of flower visitors were observed for *B. basiloba* and *B. intermedia* and were exclusively bees from the families Apidae and Halictidae (Table 3 and Figure 2). The visits to the flowers occurred mainly between 7:00 am and 2:00 pm and then until 4:30 pm at a lower frequency.

Tabela 3. Visitantes florais de *B. basiloba* e *B. intermedia* (Malpighiaceae) em um fragmento de Cerrado no Brasil Central e seus polinizadores efetivos, recompensa coletado e tamanho corporal.

Table 3. Flower visitors to *B. basiloba* and *B. intermedia* (Malpighiaceae) in a Cerrado fragment in Central Brazil and their pollination role, collected reward and body size.

Visitor	<i>B.</i> <i>basiloba</i>	<i>B.</i> <i>intermedia</i>	Reward	Size
APIDAE				
Centridini				
<i>Epicharis (Triepicharis) analis</i> (Lepeletier, 1841)	EP	EP	P-O	Medium-large
<i>Epicharis (Epicharis) bicolor</i> (Smith, 1874)	-	EP	P-O	Medium-large
<i>Epicharis (Epicharana) flava</i> (Friese, 1900)	EP	-	P-O	Medium-large
Tapinotaspidini				
<i>Paratetrapedia aff. Testacea</i> (Smith, 1854)	OP	-	O	Medium-large
HALICTIDAE				
Augochlorini				
<i>Augochloropsis aurifluens</i> (Vachal, 1903)	-	EP	P	Small
<i>Augochloropsis cfr. illustris</i> (Vachal, 1903)	-	EP	P	Small

EP = Effective pollinator, OP = Occasional Pollinator, P-O = Pollen and oil, O = Oil, P = Pollen.

PE = Polinizador efetivo, PO = Polinizador ocasional, P-O = Pólen e óleo, O = Óleo, P = Pólen.

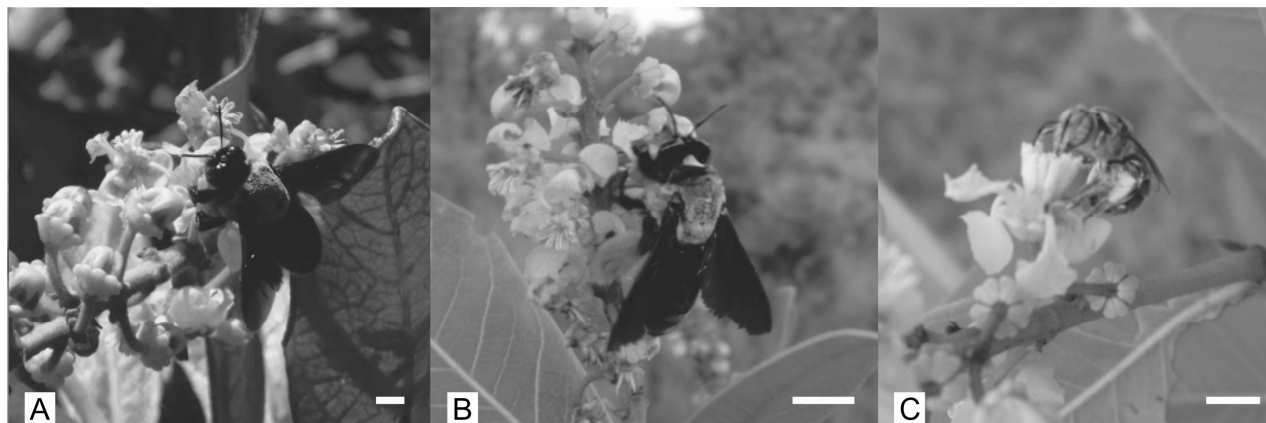


Figure 2. pollinator to *B. basiloba* (A) and *B. intermedia* (B and C). A) *Epicharis (Epicharana) flava*. B) *Epicharis (Epicharis) bicolor*; C) *Augochloropsis cfr. illustris*. Scale bar: 0.5 cm.

Figura 2. Polinizadores de *B. basiloba* (A) e *B. intermedia* (B e C). A) *Epicharis (Epicharana) flava*. B) *Epicharis (Epicharis) bicolor*; C) *Augochloropsis cfr. illustris*. Escala: 0.5 cm.

Female bees of the genus *Epicharis* were frequently seen during all periods of observation collecting pollen and oil. They approach the inflorescences in quick flights, without a pattern, landing on flowers and holding the superior petals (banner) with their mandibles. They support themselves with their hind legs on neighboring flowers or the

inferior petals of the visited flower, staying there for three or four seconds and scratching the elaiophores in the sepals, with a preference for newly open flowers. When back in flight, the collected oil was transferred to the hind legs. Individuals of the genus *Epicharis* touched the reproductive structures during oil collection, and pollen

grains were found on the ventral area and on the legs; therefore, they were considered effective pollinators. The transfer of pollen grains from the ventral part of the body to the hind legs, where they are stored and transported, occurs during the flight with quick movements, with help of the fore and midlegs. The bee *Paratetrapedia aff. testacea* Smith was an exclusive visitor of *B. basiloba*, and it collects oil in pre-anthesis flower buds. This bee lands on the flower bud and scratches the glands with its forelegs. It is considered an occasional pollinator, because it forces the opening of the petals. Bees of the genus *Augochloropsis* were observed on *B. intermedia* and collected pollen only. Because it is a small bee, the time it remained on the flower was longer. The collection of pollen was mostly performed on the stamens of the flowers.

DISCUSSION

Floral biology

The flower morphology of *B. basiloba* and *B. intermedia* follows the standard for the Malpighiaceae family, being hermaphrodite, dichlamydeae, pentamerous and zygomorphic. The flowers from these species are distinguished based on the diameter and the size of all the flower structures, with the highest values being registered for the former. In addition, other aspects, such as calyx coloration, can also be used for flower differentiation. The length of the raceme and diameter of the flowers of this species are greater than those obtained for *B. rotunda* Griseb., *B. umbellata* Mart. ex A.Juss. (Mendes et al., 2011), *B. coccolobifolia* Kunth (Benezar & Pessoni, 2006) and *B. sericea* DC. (Teixeira & Machado, 2000). The number of flowers observed in *B. intermedia* inflorescences was the highest among the cited species.

The flower morphology of Malpighiaceae is constant and seems to have been shaped by plant-pollinator interactions (Anderson, 1979; Neal et al., 1998; Endress, 2001). In the case of Malpighiaceae, the interaction occurs with oil-collecting bees. This hypothesis is

supported by the fact that New World species exhibit a zygomorphic symmetry due to the modified petal, the banner. The presence of this modified petal is interpreted as an orientation provider for landing, a positioning guide and support for the pollinator during the oil collection and the location by which the bee holds itself with its mandible (Anderson, 1979; Sazima & Sazima, 1989; Vogel, 1990; Benezar & Pessoni, 2006; Gaglianone, 2000; Sigrist & Sazima, 2004). In the Old World, the flower morphology of this family plant is different, most likely due to the absence of specific pollinators. Some species have no elaiophores, some have zygomorphic symmetry (however different form that of the tropical New World species), and some are actinomorpha (Davis et al., 2002; Davis et al., 2004; Davis, 2002). The difference in petal color is variable during the maturation phases for some flowers of the genus *Byrsonima*. The color change can occur in the whole corolla after fecundation, only in the banner or during the transition from buds to senescent flowers (Mendes et al., 2011; Benezar & Pessoni, 2006).

Reproductive system

Malpighiaceae species have strategies by which to limit self-pollination, such as the presence of a stigmatic cuticle, which can be easily broken but requires mechanical forces, which are normally provided by floral visitors, mainly oil-collecting bees. (Sigrist & Sazima, 2004).

The highest rate of fruit formation obtained from the xenogamic reproductive system was already reported for other species of the genus *Byrsonima*, such as *B. gardnerana* A. Juss. (Bezerra et al., 2009), *B. microphylla* A. Juss., *B. sericea* DC. (Costa et al., 2006), *B. umbellata* (Teixeira & Machado, 2000) and *B. coccolobifolia* (Mendes et al., 2011). However, it was not observed as an obligatory characteristic, as noted by Barros (1992) for seven species that showed some degree of compatibility. Cross-fertilization is important to promote gene flow between individuals and increase the variability within populations (Kearns & Inouye, 1993). Self-pollination

also has advantages; the transmission of alleles is guaranteed, allowing the fixation of favorable genes (Barringer, 2007). However, the offspring from related individuals are less fit than those obtained from cross-fertilization (Charlesworth & Charlesworth, 1987) and can be subjected to endogamic depression if there are deleterious genes in the population (Lloyd, 1992; Barringer, 2007).

The majority of angiosperms have mixed abilities of reproduction (self and cross), which can be demonstrated in *B. basiloba*. This strategy guarantees a high level of population adaptability to environmental conditions, which allows the species to colonize new and extensive areas (Scariot et al., 1991). Jaimes & Ramirez (1999) affirmed that self-compatible species are associated with the initial stages of succession of disturbed areas, where autogamy is selective as a colonization strategy. Self-incompatibility also guarantees reproductive success in cases of simultaneous blooming in species that share the same pollinators (Waser, 1978), as was the case for the species studied here.

Pollination

In the Jataí Ecological Station, an area of Cerrado in São Paulo state, Gaglianone (2003), recorded 14 species of bees of the genus *Epicharis* during three years of observation. She observed that there were two activity peaks of those visitors, one occurred during the beginning of the rainy season, which was associated with the peak in *B. intermedia* flower formation. This was the most visited specie, being the main source of pollen and oil to the bees. The other peak occurred at the end of the rainy season when other species of Malpighiaceae were already producing flowers. Reis et al. (2007) isolated a fatty acid from *B. intermedia* called byrsonic acid, which is responsible for the visits of the bee *Tetrapedia diversipes* Klug and other Apidae (Anthophoridae) to its flowers. *B. intermedia* is a key resource for the maintenance of pollinators in the Cerrado fragment in Rio Verde due to its broad distribution and abundance in the study area.

Teixeira & Machado (2000) observed the same behavior of *Paratetrapedia* on *B. sericea* flowers, where it collected not only oil but also pollen. The pollen collection for *Epicharis* and *Augochloropsis* was conducted actively by *buzz pollination*, which is characterized by stamen vibration by the bees. Teixeira & Machado (2000) also recorded that bees of this genus preferred flowers that opened on the same day.

CONCLUSION

The flowers of *B. intermedia* and *B. basiloba* follow the morphological pattern of the other species of Malpighiaceae the New World. The two species differ in the need for effective pollinator for reproductive success, with *B. intermedia* more dependent.

Even though small fragment where the study was conducted and having undergone intense pressure from the surrounding agricultural matrix also hosts the typical and effective pollinators, usually found in association with Malpighiaceae flowers.

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