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Floral Visitors and Reproductive Strategies in Five Melittophilous Species of Bignoniaceae in Southeastern Brazil

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ABSTRACT

In order to evaluate the pollination strategies of Bignoniaceae, the floral biology and the floral visitors in five species, three cerrado shrubs (Arrabidaea brachypoda (DC.) Bor., Jacaranda decurrens Cham., and Jacaranda oxyphylla Cham.), and two lianas from the border of a semideciduous seasonal forest (Arrabidaea samydoides (Cham.) Sandw., and Arrabidaea triplinervia H. Baill.) were studied in Botucatu, São Paulo State, Southeastern Brazil. The flowering periods were partially overlapping, especially between species in the same habitat. All the five species were functionally allogamous, melittophilous, nototribic and mainly pollinated by long tongued large bees. Some medium-sized and small pollen-foraging bees were occasional legitimate visitors, whereas others visitors were robbers/thieves. Each species showed a particular set of pollinators. Only two pollinator species were observed in more than one bignon. There was no partition of pollinators even among the species of bignons blooming at the same time at the same habitat.

Key words: *Arrabidaea*, *Jacaranda*, melittophilly, pollination, breeding system

INTRODUCTION

Bignoniaceae are often one of the most important members of Neotropical plant communities (Gentry 1988). The study of pollination strategies is of major importance in understanding the reproductive adaptation of this plant family. Studying the distribution, ecology, and co-evolutionary patterns in tropical Bignoniaceae, Gentry (1974a, 1974b, 1976) suggested that sympatric species presented species-specific niches, and that pollinator interaction mode is a determinant of intra-community bignon diversity. Co-occurring species of this family in Neotropical communities have particular forms of pollination. This can be seen in their floral variety in association to diverse pollinators such as bats, hummingbirds, moths, butterflies, and bees (e.g. Bertin 1982, Weber and Vogel 1986, Gentry 1990, Endress 1994, Barros 2001). Gentry (1976) proposed that, in general, in a certain plant community, only one bignon species of each pollination strategy would be flowering at any time. In some bignon species that share the same pool of pollinators, mainly bees, seasonal separation would also be an important isolating mechanism (Gentry 1974a, 1974b). The floral biology of bignon species has been investigated in some communities in Brazil (Yanagizawa and Gottsberger 1983, Amaral 1992 *in* Bittencourt Jr. 2003, Gobatto-Rodrigues and Stort 1992, Barros 2001, Dutra and Machado 2001, Lopes et al. 2002,

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Bittencourt Jr. et al. 2003, Bittencourt Jr. and Semir 2004, 2005).

In the Botucatu region, São Paulo State, Southeastern Brazil, species of Bignoniaceae occur in vegetation fragments (Grombone-Guaratini and Maimoni-Rodella 1995; Silberbauer-Gottsberger and Eiten 1983). In this region, five species were studied. Individuals of three shrub species (*Arrabidaea brachypoda* (DC.) Bor., *Jacaranda decurrens* Cham. and *Jacaranda oxyphylla* Cham.), occurred in a secondary cerrado vegetation; two liana species (*Arrabidaea samydoides* (Cham.) Sandw. and *Arrabidaea triplinervia* H. Baill.) were found in a semideciduous seasonal forest edge. Considering that the studied vegetation fragments were located side by side, and the available information about the adaptation of *Jacaranda* (Bittencourt 1981 *in* Bittencourt Jr. 2003, Vieira et al. 1992 *in* Bittencourt Jr. 2003, Bittencourt Jr. 2003) and *Arrabidaea* (Amaral 1992 *in* Bittencourt Jr. 2003) for bee pollinators, the similarity between their floral visitors was analyzed. This investigation was carried out aiming to describe the floral biology of these five species and to answer the following questions: Did the species flower at the same time? If so, did they share pollinators?

MATERIAL AND METHODS

The regional climate at Botucatu is humid subtropical with dry winter and rainy summer, that is, Koeppen´s Cwb (Carvalho et al. 1983). The rainy season normally starts in October and lasts until March (Tubellis et al. 1971). Cerrado and semideciduous seasonal forest are the two predominant vegetation types in this region, but they have been heavily impacted by humans and exist at the present time as often highly disturbed fragments. In cerrado areas, *Arrabidaea brachypoda* (23 individuals), *Jacaranda decurrens* (03 individuals) and *J. oxyphylla* (30 individuals) were studied, as well as, *A. samydoides* (04 individuals) and *A. triplinervia* (06 individuals) in semideciduous seasonal forest borders.

These species were analyzed for plant habit, flower traits (shape, texture, color, size, nectar and scent), length of anthesis, number of flowers per inflorescence and breeding systems, between August 1978 and December 1981. Measurements of floral parts were based on ten flowers. All the individuals were monitored every fifteen days, recording initial and final flowering periods. Flowering intensity was visually estimated. The breeding system was defined based on the automatic pollination and hand-made tests such as self-pollination, geitonogamy, and xenogamy, according to Dafni (1992). These tests were performed by isolating the flower buds in paper bags before anthesis. Subsequent fruit production was monitored until the dispersal phase. Nectar volume was sampled from ten bagged flowers with 2 μl capillary tubes and its soluble solids concentration was measured with a hand refractometer.

The presence and behavior of floral visitors were monitored by direct observation from early morning (approx. 05:30 h) to late afternoon (approx. 18:00 h), during 75 non-consecutive days along the years of study. Visits were monitored over approx. 40 h at each bignon species. The floral visitors were classified as pollinators or robbers/thieves (*sensu* Dafni 1992; Inouye 1980). The visitors were collected and identified. For each visitor species, the abundance was registered considering the number of recorded visits. For each bignon, the visitors relative abundance (RA) was calculated based on the total number of recorded visits. The visitors were considered common or occasional legitimate pollinators or robbers/thieves based on behavior and RA. The plant species were compared in relation to floral visitors presence/absence and its behavior as pollinators or robbers/thieves.

RESULTS AND DISCUSSION

Arrabidaea brachypoda and *Jacaranda oxyphylla* bloomed both in the dry and rainy seasons; the other species bloomed in the rainy season only (Fig. 1). There was partial overlapping of blooming periods, especially between species in the same vegetation type (Fig. 1 and Table 1). Anthesis was similar for all the species, starting around 06:00 h. At this time, for all the species, the stigma was receptive and the four anthers were dehisced. Flowers fell from the plants approx. 24 h after opening in *Arrabidaea* and after 36 h in *Jacaranda*.

Arrabidaea and *Jacaranda* have a dorsiventrally compressed gullet corolla (*sensu* Faegri and Pijl

1979), with membranous texture. Essential floral traits are summarized in Table 1. In open flowers, the lip shows two superior reflexed lobes and three inferior lobes that extend horizontally in the same plane as the corolla tube. In all the five species, the inferior portion of the corolla has two longitudinal folds from the fauces to the constricted region near the base of the corolla tube, forming a furrow of more intense color. This may be considered a nectar guide due to its structure and color (Kevan 1979).

Table 1 - Habit and floral characteristics of *Arrabidaea* and *Jacaranda* species (Bignoniaceae). Botucatu, SP, Brazil

	A. brachypoda	***A. samydoides***	***A. triplinervia***	***J. decurrens***	***J. oxyphylla***
Vegetation	Disturbed Cerrado	Secondary forest	Secondary forest	Cerrado	Disturbed Cerrado
Habit	Shrub (±150 cm)	Liana (± 600 cm)	Liana (±300 cm)	Shrub (± 50 cm)	Shrub (± 150 cm)
Number (#) of individuals	23	04	06	03	30
Distribution	Grouped	Scattered	Scattered	Scattered	Densely grouped
Floral traits					
Calyx					
Shape	Long tube	Shallow cup	Long tube	Shallow cup	Medium tube
Texture	Membranaceous	Membranaceous	Coriaceous	Membranaceous	Membranaceous
Color	Green	Green	Green	Dark purple	Dark purple
Corolla					
Shape*	Gullet	Gullet	Gullet	Gullet	Gullet
Texture	Thin membranaceous	Thin membranaceous	Thick membranaceous	Thin membranaceous	Thin membranaceous
Color	Lilac	Mauve	Mauve	Purplish blue	Purple
Length (cm)	3 - 4.5	4	4	4	5
Nectariferos	Cyathiformis	Cyathiformis	Cyathiformis	Pulvinate	Pulvinate
Nectar amount	5-10	5-10	5-10	Nm	Nm
Nectar centration	18 - 21	19 - 21	19 - 20	Nm	Nm
Scent	Intense and sweet	Intense and sweet	Intense and sweet	Faint and sweet	Faint and sweet
# fresh open flowers/inflorescence-day (n=10)	2-3	1-2	1-2	1-2	2-3
# flowers/inflorescence (n=10)	30 - 60	20 - 40	15 -30	15 - 20	25 - 40

**sensu* Faegri and Pijl (1979); ***sensu* Font Quer (1979); Nm: not measurable, soaked in nectariferous disk.

In all the five species, a nectariferous disk was located at the base of the ovary and produced nectar. Nectar was more abundant in *Arrabidaea* species (Table 1). In *Jacaranda*, nectar was viscous and scarce and did not accumulate at the base of the corolla. For all the species, the style was terminal and included. The stigma was bilobated with a larger inferior lobe. The stigma papillae were in the inner face of these lobes. The style lied along the dorsal surface of the corolla tube and the stigma was located directly above the didynamous stamens, which were also included and proximate to the upper corolla region. This disposition permited nototribic pollination in all the five species. In *Jacaranda*, the staminode was well developed and covered by many glandular hairs. This staminode reduced the inner corolla space. In *Arrabidaea*, the staminode was inconspicuous.

The five species have a series of floral traits characteristic of melittophily as described by Gentry (1974b) and Faegri and Pijl (1979). The flower colors and fragrances of all five species (Table 1) were attractive to bees, according to Proctor and Yeo (1973) and Kevan (1979). Nectar was the main reward for *Arrabidaea* visitors; the anthers position made pollen collection difficult. In *Jacaranda*, pollen was an additional reward for the visitors because at anther dehiscence some pollen fell on the staminode, making it more accessible to the visitors. Furthermore, this staminode could hinder access to nectar by reducing the inner corolla space. As a consequence, the visit duration and pollinator contact with the anthers and stigma increased. These events made the visits more efficient as reported by Walker-Larsen and Harder (2001) in melittophilous species of *Penstemon* (Scrophulariaceae) and by Bittencourt Jr. (2003) in melitophilous *Jacaranda racemosa*.

Table 2 - Fruit set (%) following the pollination treatments of *Arrabidaea* and *Jacaranda* (Bignoniaceae). Botucatu, SP, Brazil. (--): test not performed.

	Treatments			
	Automatic pollination	Self-pollination	Geitonogamy	Xenogamy
A. brachypoda	0 (0/27)	3 (1/35)	6 (3/35)	10 (2/20)
A. samydoides	3 (1/32)	37 (13/35)	40 (16/40)	88 (31/35)
A. triplinervia	0 (0/25)	0 (0/20)	0 (0/20)	0 (0/15)
J. decurrens	0 (0/10)	0 (0/8)	--	--
J. oxyphylla	3 (1/30)	26 (9/35)	37 (13/35)	88 (22/25)

Data in parenthesis are number of fruits/number of bagged flowers

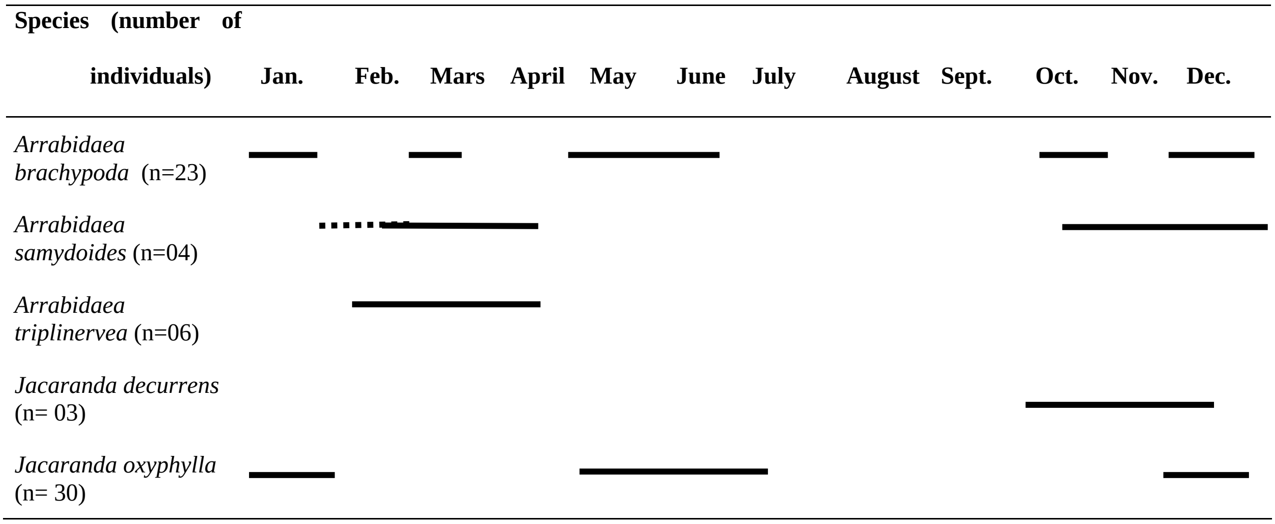

Figure 1 - Flowering phenology of five Bignoniaceae, Botucatu, SP, Brazil. Solid lines: intense flowering. Dots: scarce flowering

Arrabidaea brachypoda, *A. samydoides* and *J. oxyphylla* probably were self-compatible (Table 2), but autogamy was impaired because the position of the receptive surface of the stigma made spontaneous self-pollination difficult. In all the species, the stigma lobes temporarily closed after first contact with the floral visitors, which favored allogamy and hampers autogamy as described by Meeuse (1966) for other species with sensitive stigmas. *A. triplinervia* and *J. decurrens* were possibly self-incompatible as there was no fruit production after self-pollination (Table 2). Self-incompatibility seemed to be very frequent in Bignoniaceae (Bawa 1974, Stephenson and Thomas 1977, Petersen *et al* 1982, Bertin and Sullivan 1988, Gibbs and Bianchi 1993, 1999, James and Knox 1993, Bittencourt Jr et al. 2003, Bittencourt Jr. and Semir, 2004). Thus, the studied species could be considered as functionally allogamic, which is common among Neotropical Bignoniaceae (Gentry 1990).

Flowers of the five Bignoniaceae were visited by several species of bees (Table 3); all bee species were active predominantly between 07:00 and 15:00h. The abundance of some bees was mostly high especially in *A. brachypoda* and *J. oxyphylla* (Table 3) probably due to the grouped distribution of these species in the disturbed vegetation areas, and high number of flowers/inflorescence (Table 1). Most bees were common legitimate pollinators (genera *Bombus*, *Centris*, *Epicharis*, *Euglossa*, *Eulaema*, *Megachile*, *Melitoma,* and *Thygater*).

Table 3 - Floral visitors relative abundance (%) in five Bignoniaceae, Botucatu, SP, Brazil. 1: Common legitimate visitor; 2: Occasional legitimate visitor; 3: Robbers (R) or Thieves (T); S: small (body length < 10 mm); M: medium (10 mm ≥ body ≤ 20 mm); LA: large (body > 20 mm); L: long tongue (8 - 13 mm); ME: medium tongue (4 - 7 mm); SH: short tongue (≤ 3 mm); V: various. For each visitor species data in parenthesis are number of visits / total number of visits at the plant.

	Visitors	**Body size/ Tongue length**	**Bignoniaceae**				
			A. brachypoda	***A. samydoides***	***A. triplinervea***	***J. decurrens***	***J. oxyphylla***
1	*Bombus (Fervidobombus) atratus*	M/L	24.8 (31/125)				77.6 (125/161)
	Centris hemisiella	M/ME					5.0 (8/161)
	Centris	LA/L	4.0 (5/125)				
	Centris (Melanocentris) pectoralis	LA/L		8.0 (7/87)			
	Centris (Melanocentris) colaris	LA/L			16.0 (12/75)		
	Centris (Melanocentris) xanthoenemis	LA/L			16.0 (12/75)		
	Epicharis rustica flava	LA/L	3.2 (4/125)				
	Epicharis sp.	LA/L	4.0 (5/125)	8.0 (7/87)	16.0 (12/75)		
	Epicharis (Xanthepicharis) bicolor	M/L				21.4 (18/84)	
	Euglossa (Euglossa) cordata	M/L		11.5 (10/87)			
	Euglossa (Euglossa) sp.	M/L				44.0 (37/84)	
	Euglossa sp.	M/L			26.6 (20/75)		
	Eulaema (Apeulema) nigrita	M/L	1.6 (2/125)				
	Megachile sp.	M/ME					1.9 (3/161)
	Melitoma sp.	M/L					5.0 (8/161)
	Thygater analis	M/L					1.2 (2/161)
2	*Augochlora* (cf.) *esox*	S/ME	8.0 (10/125)				
	Ceratina (Crewela) sp. 2	M/ME				15.5 (13/84)	
	Chloralictus sp.	S/SH	6.4 (8/125)				
	Epicharis (Epicharitides) sp.	M/ME	1.6 (2/125)				
	Exomalopsis (Megamalopsis) lvofasciata	S/ME	1.6 (2/125)				
	Mesoplia rufipes	M/ME					3.7 (6/161)
	Trigona (Trigona) hyalenata	S/SH	5.6 (7/125)				
3	*Ceratina (Crewella)* sp. 1 (T)	M/SH	5.6 (7/125)	2.3 (2/87)	2.6 (2/75)	14.3 (12/84)	
	Oxaea flavescens (R)	M/ME	13.6 (17/125)	34.5 (30/87)	6.6 (5/75)	4.8 (4/84)	1.8 (3/161)
	Paratrigona lineata lineata (T)	S/SH	4.0 (5/125)	2.3 (2/87)	2.6 (2/75)		
	Trigona (Trigona) spinipes (T)	S/SH	5.6 (7/125)				3.7 (6/161)
	Xylocopa (Megaxylocopa) frontalis (R)	LA/ME	4.8 (6/125)	2.3 (2/87)			
	Xylocopa (Megaxylocopa) virescens (R)	LA/ME		13.8 (12/87)			
	Xylocopa (Schosnheraia) (cf.) *macrops* (R)	LA/ME			9.3 (7/75)		
	Xylocopa (Megaxylocopa) sp. (R)	LA/ME		13.8 (12/87)			
	Butterflies (T) and beetles (R)	V/V	5.6 (7/125)	3.4 (3/87)	4.0 (3/75)		

They were of medium to large size, principally nectar collectors and visited the flowers nototribically. These bees were considered efficient pollinators because of their abundance at the flowers and also because they could easily contact anthers and stigmas. Species of *Bombus*, *Centris*, *Epicharis* and *Eulaema* (Barros 2001, Bittencourt Jr. 2003) and *Euglossa* (Bittencourt Jr. 2003) were also reported to be efficient pollinators of *Tabebuia*. Species of *Bombus*, *Centris* and *Xylocopa* were considered as the main pollinators of the Bignoniaceae family at cerrado vegetation (Silberbauer-Gottsberger and Gottsberger 1988). Nevertheless, at *Arrabidaea* and *Jacaranda* flowers, *Xylocopa* was never observed performing legitimate visits (Table 3).

There was also occasional legitimate pollination (Table 3) performed by the small and medium-sized pollen-foraging bees (*Augochlora*, *Ceratina* sp 2, *Chloralictus*, *Exomalopsis*, *Epicharis (Epicharitides)* sp., *Mesoplia*, and *Trigona hyalenata*), which collected pollen directly from the anthers, occasionally touching the stigma. Among the visitors, there were two larceny groups: robbers and thieves. Robbers were large and medium-sized bees that collected nectar by perforating the corolla base (*Xylocopa sp., X. frontalis*, *X. macrops*, *X. virescens* and *Oxaea flavescens*). The same larceny behavior was registered for *Xylocopa* sp. in *Jacaranda racemosa* and species of *Tabebuia* (Bittencourt Jr. 2003) and for *Oxaea flavescens* in species of *Tabebuia* (Bittencourt Jr. 2003). Thieves were small and medium-sized bees that collected pollen directly from the anthers, never touching the stigma receptive surface (*Paratrigona*, *Trigona spinipes*, and *Ceratina* sp 1). *Trigona spinipes* was likewise observed thieving *Tabebuia* flowers (Barros 2001, Bittencourt Jr. 2003).

Arrabidaea brachypoda had the greatest richness of bee visitors (15 species) and *J. decurrens* the lowest (5 species) (Table 3). The other plants showed intermediate values: 8 species for *A. triplinervia* and *J. oxyphylla*, and 9 species for *A. samydoides*. *A. brachypoda* and *J. oxyphylla* had the same number of common legitimate visitors (5 species). However, the total richness was higher for *A. brachypoda* considering that five occasional legitimate visitors also visited it whereas *J. oxyphylla* was visited by only one (Table 3). The pollinators richness can be related to reward offer, because *A. brachypoda* and *J. oxyphylla* have large inflorescences and formed dense populations at the studied sites (Table 1). Furthermore, they were possibly more accessible as they occurred preferentially in sparsely vegetated cerrado areas. This pattern of resource offer was generally associated with pollination by different bee species (Frankie 1976).

The five Bignoniaceae could be classified as non-promiscuous (*sensu* Percival 1965), as the floral characteristic gullet corolla and the location of the stamens restricted the access to rewards to certain groups of visitors. Most of the pollinators in this study were long tongued medium sized to large bees (Table 3) that according to Baker and Hurd (1968), Stebbins (1970) and Faegri and Pijl (1979) showed adaptive relationships with tubular flowers during their evolutionary history. According to Gentry (1990) and Endress (1994), these bees were the main pollinators of melittophillous Bignoniaceae.

For four of the studied species, there were more pollinating species of bees than robbing species; only *A. samydoides* had more robbing than legitimately visiting bee species with high RA (Table 3). Its shallow bowl-shaped calyx (Table 1) was probably not a barrier to the robbing bees; the other *Arrabidaea* species have long tubular calyces, which probably provided better protection against the robbers. The lowest robbers richness was seen in *Jacaranda*. This was possibly due to the lack of available nectar in the flowers (Table 1) and to the hairy staminode that made the access to the floral tube difficult. The results showed that each Bignoniaceae had a particular set of pollinators (Table 3). Some overlapping occurred between *J. oxyphylla* and *A. brachypoda,* which presented *Bombus atratus* in common, and between the three *Arrabidaea* species in relation to *Epicharis* sp. *Jacaranda decurrens* was very different by presenting a unique set of visitors.

The results indicated that there was very little overlapping in the species of bees between any of the bignons even though the plants were all melittophilous and had very similar floral morphologies. The differences between plants lied, probably, in the accessibility and quality of the nectar. This feature needs further investigation. There are phenological and habitat differences between some of the species as well, but even when species flower at the same time in the same habitat, they attract different suites of bees. This can be an evolutionary consequence of competition to reduce the negative interaction between coexisting species (Stone et al. 1998). It is well known that to avoid competition plants may differ in the pollinators they recruit and so have independent pollen vectors (Heinrich 1976, Pleasants 1980, Rathcke 1988). Therefore, for the studied plants, the interference in pollination seemed to be minimized mainly as a result of interspecific differences in flower visitor assemblages and less by phenological strategy or seasonality as pointed out by Gentry (1974a, 1990) in Neotropical melittophilous Bignoniaceae.

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RESUMO

Com objetivo de avaliar as estratégias de polinização de espécies de Bignoniaceae, foram estudados a biologia floral e os visitantes florais de cinco espécies, três arbustivas do cerrado (*Arrabidaea brachypoda* (DC.) Bor., *Jacaranda decurrens* Cham. e *Jacaranda oxyphylla* Cham.) e duas lianas da orla da floresta estacional semidecidual (*Arrabidaea samydoides* (Cham.) Sandw. e *Arrabidaea triplinervia* H. Baill.), na região de Botucatu (22^{o}52’20” S e 48^{0}26’37” W), estado de São Paulo, sudeste do Brasil. Os períodos de florescimento, principalmente entre espécies do mesmo habitat, apresentaram sobreposição parcial. Observou-se que as cinco espécies são alogâmicas funcionais, melitófilas, nototríbicas, polinizadas principalmente por abelhas grandes de língua comprida. Algumas abelhas coletoras de pólen de tamanho médio e pequeno atuaram como polinizadoras ocasionais, enquanto outros visitantes foram pilhadores. Cada uma das Bignoniaceae apresentou um conjunto particular de polinizadores havendo apenas duas espécies comuns a mais de uma delas. Não houve partilha de polinizadores mesmo entre bignoniáceas que, no mesmo habitat, apresentaram períodos de florescimento simultâneo.

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