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Original article

Africanized honey bees pollinate and preempt the pollen of *Spondias mombin* (Anacardiaceae) flowers

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Abstract – The invasion of generalist Africanized honey bees may change certain plant–pollinator interactions. We evaluated the preemption by honey bees and the exploitative competition with native bees on a tree with nocturnally dehiscent small flowers. Our main objectives were to quantify pollen production and harvesting, to verify whether honey bees exploitatively compete with native bees and to identify the effective pollinators of *Spondias mombin*. The nocturnally dehiscent flowers were pollen depleted by honey bees and attracted various nocturnal and diurnal bee species. A threefold increase in native bee abundance was produced by delaying pollen availability and by preventing the preemption of pollen by honey bees. The results suggest that honey bees reduce the foraging benefit of late-arriving native bees. Honey bees and *Scaptotrigona aff. tubiba* were regarded as the main effective pollinators of *S. mombin* due to their abundance, behavior, and ability to visit a large number of flowers.

Apis mellifera / pollen depletion / stingless bees / nocturnal bees / pollination

1. INTRODUCTION

Trees with small flowers produce a large quantity of floral resources clustered in rich inflorescences that are exploited by highly eusocial bees in tropical rainforests (Ramalho 2004). These bees have a tight association with these plants that provide a large amount of the food necessary to maintain their perennial colonies. In the Atlantic Neotropical forest, these resources are harvested mainly by stingless bees and only rarely by solitary bees (Ramalho 2004). However, after the African honey bees, *Apis mellifera scutellata* Lepeletier, invaded Neotropical ecosystems, a high overlap in food plant use with certain stingless bees was indicated (Sommeijer et al. 1983; Roubik 1989; Biesmeijer and Slaa 2006). It has also been observed that invasion of generalist Africanized honey bees can affect specific plant–pollinator interactions (Roubik 1996; Butz-Huryn 1997; Menezes et al. 2007). Most authors agree that honey bees are not particularly aggressive while foraging and the impact occur primarily through exploitative competition (Goulson 2003; Roubik 2009; Roubik and Villanueva-Gutiérrez 2009). The foraging of Africanized honey bees and stingless bees occur mainly on flowers with non-specialized morphological features (i.e., radial symmetry, open corolla, and exposed fertile structures) (Roubik 1989), which are common in trees with small flowers.

Anacardiaceae is a plant family which comprises several taxa with the floral traits men-

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tioned above (Mitchell 1997). The pollen resources produced by this group of plant is among the highly used by Africanized honey bees (Roubik 1988; Roubik and Villanueva-Gutiérrez 2009). *Spondias mombin* L. is one of the Anacardiaceae species widespread in and native to the lowland tropical rainforests of Mexico, Central America and South America. In Brazil, *S. mombin*, one of the few forest tree species used as a fruit crop with a potential for expansion, occurs in the north and northeast, where its fruits are known as "taperebá" and "cajá," respectively. This species produces many small flowers in large inflorescences, and bees in general, which forage primarily for pollen, are regarded as their pollinators (Roubik 1995). Populations of *S. mombin* display seasonal and synchronous patterns in flowering phenology (Adler and Kielpinski 2000) that can be more efficiently exploited by bees. There is no information concerning the pollination biology of *S. mombin*, and only superficial observations on the matter have been made (Lozano 1986; Stacy et al. 1996; Nason and Hamrick 1997).

We investigated the pollination biology and breeding system of *S. mombin* within an experimental area of the tropical Atlantic rainforest in northeastern Brazil. We asked the following questions: (1) How much pollen do androgynous and staminate *S. mombin* flowers produce? (2) How much pollen is harvested by honey bees? (3) Do Africanized honey bees exploitatively compete with native bees? and (4) What species are the flower visitors and effective pollinators of *S. mombin*?

2. MATERIALS AND METHODS

2.1. Studied species

S. mombin displays a diversified sexual expression throughout its occurrence in the Neotropical region. Populations of *S. mombin* are dioecious in Mexico (Pennington and Sarukhan 2005) and monoecious in Costa Rica (Bawa and Opler 1975). In Panamá, Croat (1978) reported generally androgynous flowers (with few pistillates). However, in Colombia, Lozano

(1986) observed four types of flowers: androgynous, staminate, and two variations of pistillate, one with anthers lacking pollen grains and the other with deformed and sterile pollen grains. The many flower types and potential breeding systems in *S. mombin* suggest that there are hybrids or multiple species and deserve thorough studies.

Nevertheless, we verified that our studied specimens were andromonoecious. The staminate flowers bore a pistillodium, and the androgynous flowers displayed conspicuous styles and stigmata (Figure 1). Both flower types were pentamerous and actinomorphic, with a white corolla and ten stamens bearing dorsifixed anthers with longitudinal dehiscence. The nectarless flowers opened at night, a few hours before dawn, and lasted 2 days.

2.2. Study area

This study was carried out at the experimental research station of Mangabeira (07°11′52″ N; 34°48′42″ W), a property of the Empresa Estadual de Pesquisa Agropecuária da Paraíba (EMEPA-PB), João Pessoa, PB, Brazil. We conducted our observations from 2007 to 2010 during the blooming season (Sep–Dec). The experimental station covers 260 ha close to a conserved fragment of tropical rainforest. The following crops are cultivated in the area: *Anacardium occidentale* L., *Bixa orellana* L., *Eugenia uniflora* L., *Hancornia speciosa* Gomes, *Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg., *Malpighia emarginata* DC., *Mangifera indica* L., *Psidium guajava* L., *Spondias cytherea* Sonn., and *S. mombin* L. *S. mombin* is cultivated at three sites in the experimental station and composed by a germoplasm bank with seedlings and different clones propagated by grafting and cuttings, totaling 128 plants.

The climate of the region is of the As' type (warm and wet), with a relative humidity of approximately 80% and annual temperature of 22–26°C (Köppen). The mean annual rainfall ranges from 1,500 to 1,700 mm (Feliciano and Melo 2003).

2.3. Flower and pollen production

The number of flowers produced per inflorescence was counted; open flowers, buds and branches
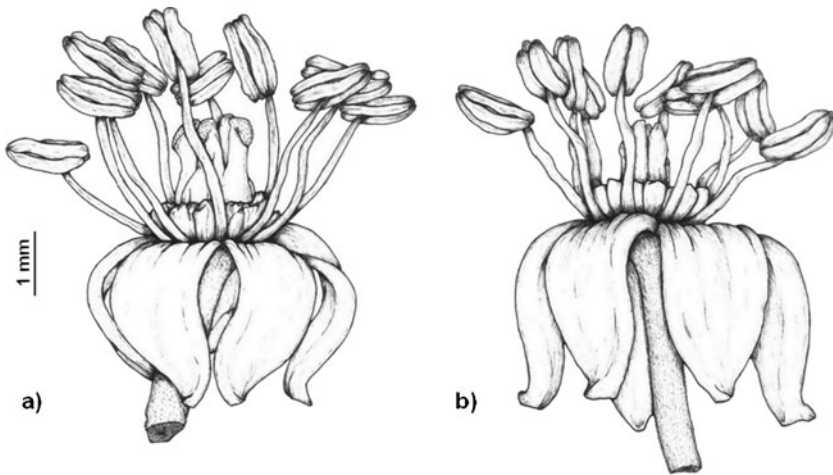
Figure 1. The flowers of *S. mombin* from a tropical Atlantic rainforest area in João Pessoa, Paraíba, Brazil. **a** Androgynous flower. **b** Staminate flower.

constituted by androgynous and staminate flowers were included in this count. Morphological and morphometric descriptions of the floral types were made using fresh and fixed materials in 70% alcohol under a stereomicroscope (MZ12 Leica®).

The number of pollen grains produced by the androgynous and staminate flowers was determined by a direct count. Five anthers of each floral bud were removed and placed in a glycerin drop on a millimetric slide. The pollen grains were removed and counted under a stereomicroscope. The number of pollen grains produced per flower type was determined by multiplying the mean number of pollen grains per anther by ten. By multiplying the number of pollen grains per flower by the number of flowers per inflorescence, we estimated the number of pollen grains per whole inflorescence.

2.4. Breeding system

The breeding system was determined through cross- and open pollination treatments. The inflorescences used in the cross-pollination treatments, including both pollen donors and receivers were bagged before anthesis to avoid pollinator contact and a loss of pollen grains. The crosses were performed between clone plants and between non-clone plants. The crosses between clones were made

in 12 inflorescences and four plants (a total of 1,021 hand-pollinated flowers), and the crosses between non-clones were made in six inflorescences and six plants (1,022 flowers). In open pollination treatments, 11 marked inflorescences (4,580 flowers) distributed in four plants remained exposed to flower visitors. The numbers of initial (immature) fruits and mature fruits were counted 2 days and approximately 90 days, respectively, after the end of anthesis. The numbers of immature and mature fruits per inflorescence were used to calculate the fruit survival rate.

To determine the requirements of pollinators, wind pollination treatments were performed. Eighteen inflorescences were bagged at pre-anthesis via tulle cloth with openings of about one square millimeter in size. Flower visitors thus had no access to the flowers; however, there remained the possibility of wind action. The mature fruits were counted and the fruit set rate was estimated using the average number of androgynous flowers per inflorescence.

2.5. Flower visitors

The number of flower visitors was recorded during the flowering seasons of 2007, 2008 and 2009. A total of 25 inflorescences distributed in 10 days and randomly chosen in different plants were observed throughout the first day of anthesis, starting before

dawn at 0300 hours. The richness of the flower visitors and the frequency of each bee species were recorded continuously from 0400 to 1700 hours daily. Voucher specimens were deposited in the Entomological Collection of the Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba.

2.6. Honey bee foraging and pollen harvesting

The number of individuals immediately (~10 s) visiting a single inflorescence and the number of flowers visited per minute by honey bee workers at the peak of visitation were recorded. Honey bees with huge pollen loads were captured and their pollen loads were removed to determine the number of pollen grains collected from flowers at the peak of activity. In addition, fidelity to *S. mombin* flowers was verified through pollen analysis of the honey bee pollen loads under a microscope. The pollen loads were placed within a 0.5-mL glycerin lactic acid solution (3:1) in a 1.5-mL Eppendorf tube. The solution was sonicated in a vortex stirrer for 5 min, and an aliquot was counted in a Neubauer chamber.

The availability of pollen grains was determined before, during and at the end of honey bee foraging at four 30-min intervals: 0400–0430, 0430–0500, 0500–0530, and 0530–0600 hours. In each interval, the pollen grains of two flowers sampled in six different days from six plants (12 flowers per interval) were directly counted on millimetric slides under a stereomicroscope.

To estimate how many honey bee pollen loads an inflorescence could provide, the following equation was used:

$$N_{PL} = \frac{FI(PG_{0400} - PG_{0530})}{PL},$$

where FI is the mean number of flowers per inflorescence, PG_{0400} is the mean number of pollen grains that remained in flowers at 0400 hours (when there had been no honey bee visits), PG_{0530} is the mean number of pollen grains that remained in flowers at 0530 hours (after honey bees' visits), and PL is the mean number of pollen grains gathered in the honey bee pollen loads.

2.7. Late pollen availability

To verify the effect of the premature foraging pattern of honey bees on native bee foraging, the abundance and richness of flower visitors on *S. mombin* inflorescences were analyzed under two simultaneous temporal treatments of pollen availability in 2010: natural pollen availability (NPA; control) and late pollen availability (LPA). In the NPA treatment, the flower visitors were recorded in seven plants and 5 days between 0300 and 0900 hours, on a total of 16 inflorescences, sampling the natural visitation rate. In LPA, the flower visitors were recorded in six plants and 5 days, on a total of 17 inflorescences bagged at pre-anthesis with tulle cloth to avoid flower visitors in the first hours of anthesis and delaying resource availability. The inflorescences were unbagged at 0600 hours, and the flower visitors were recorded until 0900 hours. Some samples of both treatments were prepared on the same plant. In both treatments, the flower visitors were counted per minute, and the data were grouped in 15-min intervals.

2.8. Statistical analysis

To compare the number of androgynous and staminate flowers produced per inflorescence, the number of pollen grains produced per androgynous and staminate flower and the size of their floral parts, the *t* test for independent samples was used. A Shapiro–Wilk test was used to check data normality. A non-parametric Mann–Whitney test was used to compare the non-normal data for pistil and pistillodium length. The mean number of pollen grains in the different anthesis phases (bud, 0400, 0430, 0500, and 0530 hours) was compared using a one-way analysis of variance (ANOVA). The outliers were removed from the sampling for this analysis. To compare the abundance of honey bees, native bees and Diptera in relation to the temporal treatments of pollen availability, the two-way ANOVA followed by Tukey's post hoc test was applied. Homogeneity of variance and residual normality was reached by transforming the data into natural logarithms. Chi-square test (χ^2) with Yates correction was used to compare the initial fruit set, mature fruit set and fruit survival rate between all the three treatments (open pollination, non-clone crosses, and clone crosses).

The number of fruits was used in the calculations. Statistical analyses were performed with STATISTICA 6.0 (Statsoft Inc.).

3. RESULTS

3.1. Flower and pollen production

S. mombin produced androgynous and staminate flowers on the same inflorescence. Staminate flowers were generally distributed in the basal branches of the inflorescence; the androgynous flowers were distributed from the middle to the apex. Inflorescences presented a mean of 1,708 flowers (SD±587, $n=13$), with 935±275 (55%) androgynous and 773±426 (45%) staminate flowers. There was no significant difference between the number of androgynous and staminate flowers ($t=1.154$; $P=0.262$). In addition, the size of the floral parts of the androgynous and staminate flowers did not differ significantly, but the pistils were significantly longer than the pistillodia (Table I).

Androgynous flowers produced an average of 12,357 (±2016; $n=18$) pollen grains, and staminate flowers produced 12,234 (±1523; $n=18$) (Figure 2). No significant difference was found ($t=0.205$; g.l.=34; $P=0.838$). Thus, a S.

mombin inflorescence produced $21×10^6$ pollen grains on average.

3.2. Breeding system

S. mombin is self-incompatible and dependent on pollinators to set its fruit. The initial and mature fruit set were significantly higher in the non-clone cross treatment (n) than in the open pollination treatment (o) and in these were higher than in the clone cross-treatment (c) (Table II). However, the fruit survival rate was significantly higher in o followed by n and by c.

Only 0.02% of the mature fruit set was obtained from wind pollination treatments.

3.3. Flower visitors

During 3 years of observation (2007–2009), S. mombin flowers attracted mainly bees, which foraged for pollen as a floral resource. Among the flower visitors, 92.7% were Apoidea (bees), 4.5% Diptera, 1.2% Formicidae, 0.9% Vespidae, and 0.8% Curculionidae. Seventeen bee species were recorded during the entire study period, and the Africanized honey bee A. mellifera showed an extraordinarily high relative frequency (71%) (Table III).

Table I. Number and dimension of the floral structures of androgynous and staminate flowers of *Spondias mombin* from a tropical Atlantic rainforest area in João Pessoa, Paraíba, Brazil.

Floral structures	Androgynous flowers		Staminate flowers		Statistics	
	Number	Dimension (mm; $n=10$)	Number	Dimension (mm; $n=10$)	t	P
Calyx (sepals)	5		5			
Corolla (petals)[a]	5	4.1±0.24	5	4.0±0.15	1.326	0.205
Stamens[b]	10	3.3±0.14	10	3.2±0.11	1.054	0.306
Anthers[b]		1.3±0		1.3±0		
Pistil/ pistillodium[b]		1.9±0.08		1.2±0.13	100.00	0.0001
Carpels/locules	3–5					
Ovules	3–5					

[a] Width

[b] Length
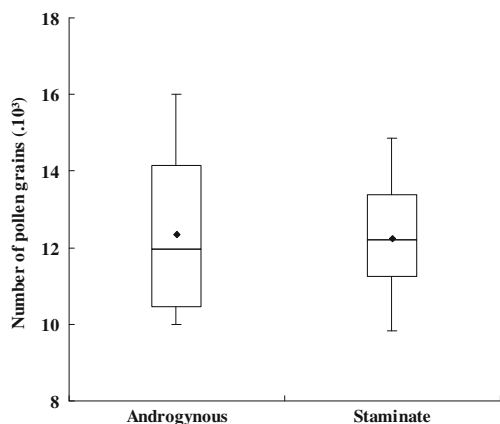
Figure 2. The number of pollen grains produced per *S. mombin* flower type ($n=18$) in a tropical Atlantic rainforest area in João Pessoa, Paraíba, Brazil (mean, median, quartiles, minimum, and maximum).

Nocturnal and crepuscular bees, *Megalopta amoena* Spinola and *Ptiloglossa goffergei* Moure, visited the *S. mombin* flowers before dawn (0400 hours). Honey bees initiated their intensive visitation several minutes later, just before dawn (0420 hours). Because the data of flower visits were grouped into 30-min intervals, the visits of the nocturnal and crepuscular bees and honey bees appeared at the same point (at the 0400–0430-hour interval) in the diagram (Figure 3). The peak of visitation was at 0430 hours; after 0530 hours, there were only sporadic visits. After 1300 hours, no more visits were recorded. The stingless bees *Frieseomelitta doederleini* Friese, *Scaptotrigona aff. tubiba* Smith, *Trigona spinipes* Fabricius, *Trig-*

ona fuscipennis Friese, and *Plebeia flavocincta* Cockerell, as well as other bee species, visited the flowers after the honey bees with low frequency (Figure 4). Furthermore, no aggressive behavior was observed between bee species. Nevertheless, all bee species visitors touched the stigmata and were therefore regarded as *S. mombin* pollinators.

3.4. Honey bee foraging and pollen harvesting

The mean number of honey bee individuals on a single inflorescence at the peak of visitation was 15 (±6.3; $n=10$). Furthermore, these bees visited an average of 21 flowers per minute ($n=22$) and stored in their pollen loads 248,680 pollen grains ($\pm120,933$; $n=9$) from *S. mombin* flowers per foraging trip.

Honey bees foraged intensively and quickly for the pollen of *S. mombin* (Figure 5). Before the honey bee visits, approximately 1 h after the opening of the flowers (at 0400 hours), 67% of the total pollen grains remained in the flowers, showing that nocturnal visits and the wind had already removed some pollen from the flowers. However, 1 h later, at the end of honey bee visits (at 0500 hours), only 5.5% of the total pollen content remained, and this reached 4.7% by 0530 hours.

The high and low outliers in the sampling at the 0400-hour interval showed that, due to the nocturnal visits, the number of pollen grains in a few flowers was close to that of flowers at the bud stage or was low. Similarly, at 0430 hours, data outliers are due to a small variation in time

Table II. Cross-pollination and open pollination treatments on the flowers of *S. mombin*.

Pollination treatments	infl	f	i	m	i/f	m/f	m/i
Open pollination	11	4,580	789	121	0.172 a	0.026 a	0.153 a
Cross-pollination between clones	12	1,021	91	2	0.089 b	0.002 b	0.022 b
Cross-pollination between non-clones	6	1,022	479	47	0.469 c	0.046 c	0.098 c

Different letters in each column mean significant differences between treatments ($P<0.05$)

infl number of inflorescences, *f* number of flowers, *i* number of initial (immature) fruits, *m* number of mature fruits, *i/f* initial fruit set, *m/f* mature fruit set, *m/i* fruit survival rate

Table III. Total abundance of bee species and their relative frequency at inflorescences of *Spondias mombin* in a tropical Atlantic rainforest in João Pessoa, Paraíba, Brazil from 2007 to 2009 and in the two temporal treatments of pollen availability (NPA and LPA, 2010).

Bee species		Number (%)		
		2007–2009	NPA	LPA
APIDAE				
APINAE				
Apini	*Apis mellifera* Linnaeus, 1758	738 (71.4)	1319 (66.1)	40 (1.8)
Meliponini	*Frieseomelitta doederleini* (Friese, 1900)	55 (5.3)	14 (0.7)	30 (1.4)
	Scaptotrigona aff. tubiba Smith, 1863	10 (1.0)	617 (30.9)	1857 (83.6)
	Trigona fuscipennis Friese, 1900	9 (0.9)	–	–
	Trigona spinipes (Fabricius, 1793)	17 (1.6)	8 (0.4)	113 (5.1)
	Plebeia flavocincta (Cockerell, 1912)	33 (3.2)	5 (0.3)	2 (0.1)
Exomalopsini	*Exomalopsis auropilosa* Spinola, 1853 and *E. analis* Spinola, 1853	22 (2.1)	2 (0.1)	64 (2.9)
Centridini	*Centris* sp.	–	–	1 (0.04)
Xylocopinae				
Xylocopini	*Xylocopa grisescens* (Lepeletier, 1841)	17 (1.6)	–	–
	Xylocopa cearensis Ducke, 1910	8 (0.8)	–	–
Colletidae				
Diphaglossinae				
Caupolicanini	*Ptiloglossa goffergei* Moure, 1953	22 (2.1)	2 (0.1)	–
Hylaeinae				
	Hylaeus sp.	8 (0.8)	–	20 (0.9)
Halictidae				
Halictinae				
Halictini	*Dialictus opacus* (Moure, 1940)	22 (2.1)	10 (0.5)	88 (4.0)
Augochlorini	*Megalopta amoena* Spinola, 1853	10 (1.0)	16 (0.8)	–
	Augochlora sp. 1 and sp. 2	62 (6.0)	3 (0.2)	5 (0.2)

of foraging by the honey bees on different days. Significant differences in the number of remaining pollen grains per flower were found by comparing buds and 0400-hour flowers with the other time intervals (ANOVA: $F=371.94$; $df=4.73$; $P<0.001$).

Regarding honey bee visitation time, the remaining number of pollen grains per flower, the number of flowers per inflorescence and the number of pollen grains per pollen load, it is possible to estimate that a single inflorescence can offer enough pollen grains to fill 52 honey bee pollen loads.

3.5. Late pollen availability

There was no significant difference in the total abundance of flower visitors between the temporal treatments of pollen availability NPA and LPA ($F=0.053$; $df=1.93$; $P=0.818$). However, the abundance of the most representative flower visitor groups (honey bees, native bees and Diptera) was

Figure 3. The frequency of honey bees and other flower visitors at the inflorescences of *S. mombin*, grouped into 30-min intervals.
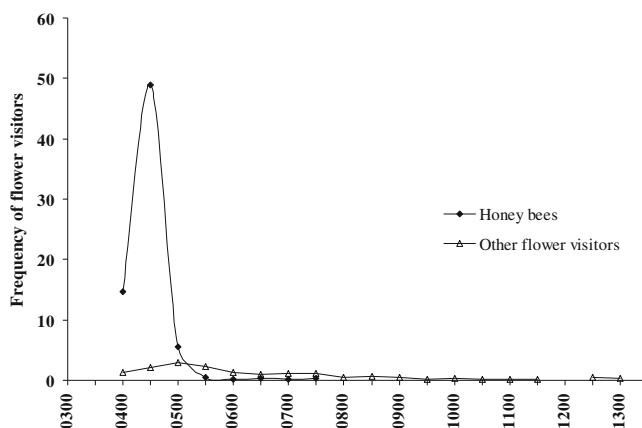

significantly different in the comparison of NPA and LPA (ANOVA: $F=31.331$; $df=2.93$; $P< 0.001$) (Figure 6). Nevertheless, a significantly higher honey bee abundance in the NPA treatment was encountered ($P<0.001$). The same was observed for native bees, but their abundance was higher in the LPA treatment ($P<0.001$). No significant difference in abundance was observed between the treatments for Diptera ($P=0.753$). Furthermore, in NPA, the honey bees (66%) were more abundant than the native bees ($P=0.001$) and Diptera ($P<0.001$). In LPA, the native bees were more abundant ($P<0.001$ compared with honey bees and $P=0.044$ compared with Diptera). In this treatment, a decrease of 95% in honey bee

abundance was observed as well as a threefold increase in the native bee abundance.

Among native bees, the stingless bee *Scapto-trigona aff. tubiba* was the most abundant in NPA and LPA (31% and 84%, respectively) (Table III). The peak of visits in the NPA treatment was reached at 0430 hours (Figure 7a), when the highest honey bee frequency occurred (Figure 7b), as also shown in the 3-year sampling (Figure 3). The second peak in the NPA, at 0600 hours, was due to *Scaptotrigona aff. tubiba* (Figure 7a, b). This occurred because these bees were also foraging at the unbagged inflorescences of LPA and were attracted to adjacent flowers of the NPA. In the LPA, *Scaptotrigona aff. tubiba*

Figure 4. The frequency of stingless bees, honey bees and nocturnal and crepuscular bees on inflorescences of *S. mombin*, grouped into 10-min intervals, during the first 2 h of visitation (0400–0600 hours) in a tropical Atlantic rainforest area in João Pessoa, Paraíba, Brazil.
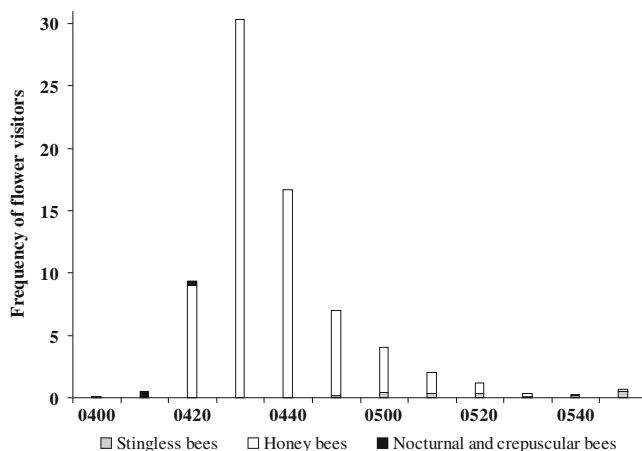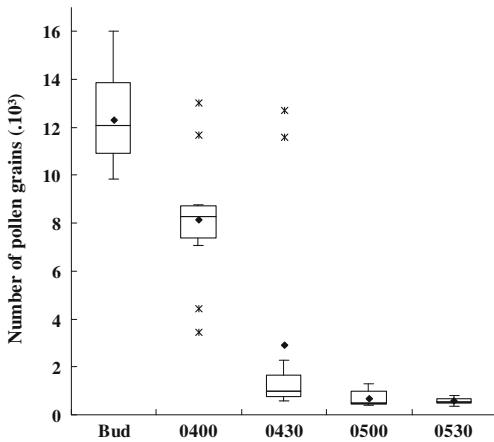
Figure 5. The number of pollen grains present in the flowers of *S. mombin* before anthesis (buds; *n*=36) and during flower visitors' activity, in 30-min intervals from 0400 to 0530 hours (*n*=12 for each interval; mean, median, quartiles, minimum, and maximum; outliers).

was the most frequent species soon after unbagging the inflorescences at 0600 hours (Figure 7c).

4. DISCUSSION

S. mombin is a synchronous flowering tree with nocturnally dehiscent flowers that produce a rich pollen resource and attract nocturnal and diurnal bee species, mainly honey bees and stingless bees. Thus, *S. mombin* flowers were attractive to the nocturnal and crepuscular bees

M. amoena and *P. goffergei*. According to Wcislo et al. (2004), *Spondias* pollen grains are used by *Megalopta* species, but there are no records of *Ptiloglossa* species as Anacardiaceae flower visitors. Moreover, *M. amoena* and *P. goffergei* initiated foraging on *S. mombin* before the honeybees did, collecting large amounts of pollen grains by attachment to the thorax and the scopa.

Although the nocturnal and crepuscular bees foraged earlier and accessed the flowers at their time of highest pollen presentation, Africanized honey bees were the most abundant visitors, depleting the pollen grains in a short period at dawn. Later, other native bees, even stingless bees, foraged with low frequency on the pollen-depleted flowers. Nocturnal flowers may be visited heavily by honey bees in early morning (Roubik 1988) and some stingless bees (e.g. *Melipona*) practice the same strategy (Roubik 1989).

In tropical Atlantic rainforests, trees with small flowers are known for being highly visited by stingless bees (Ramalho 2004). Stingless bees with large populations depend on the exploitation of rich floral resources to maintain their large perennial colony biomass. This is likely provided by *S. mombin*, a canopy species regarded as important for stingless bees, including *Scaptotrigona* Moure (Sommeijer et al. 1983; Absy et al. 1984; Teixeira et al. 2007; Marques-Souza et al. 2007). However, in this study only 5% of the pollen grains produced by

Figure 6. The abundance (natural logarithms of the numbers) of the most representative groups of flower visitors on *S. mombin* inflorescences in relation to the two temporal treatments of pollen availability (NPA and LPA; ANOVA: *F*=31.331; g.l.=2. 93; *P*<0.001).
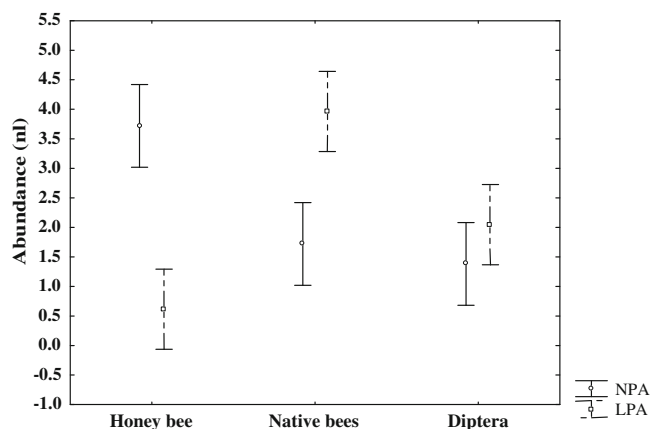
Figure 7. The frequency of flower visitors of *S. mombin* in 15-min intervals (0400–0900 hours); **a** the total number of individuals under the two temporal treatments of pollen availability (NPA and LPA); **b** the mean frequency of honey bees and *Scaptotrigona aff. tubiba* in NPA; and **c** the mean frequency of honey bees and *Scaptotrigona aff. tubiba* in LPA.
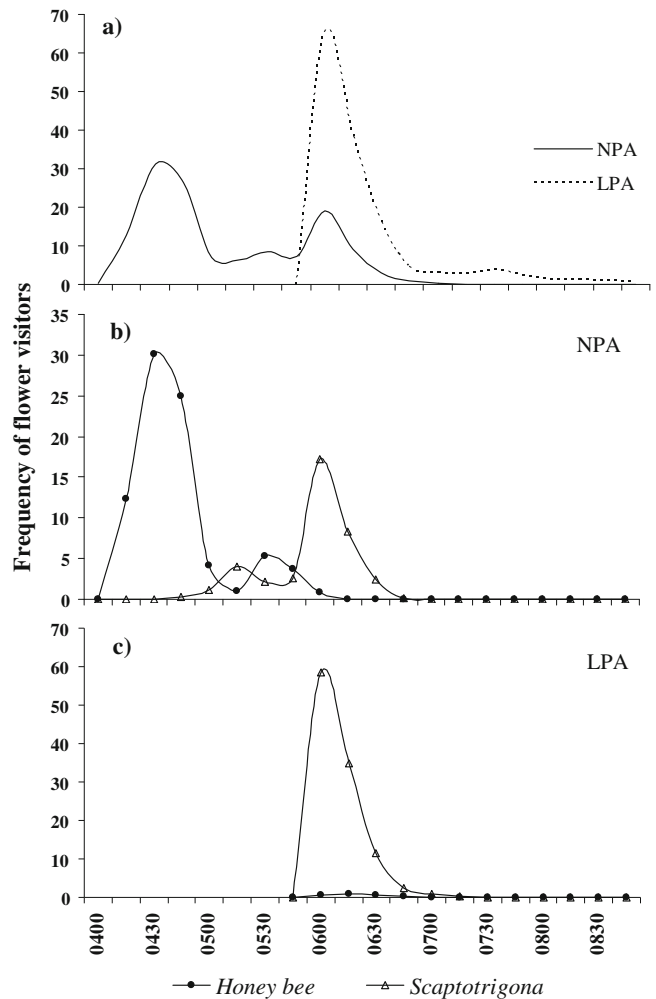
the flowers were left to the stingless bees after the impressive preemption by honey bees. Furthermore, in the experiment of late pollen availability, we observed a threefold increase in native bee abundance. Thus, the results indicate that the preemption by Africanized honey bees reduced the foraging benefit of the late-arriving stingless bees, particularly *Scaptotrigona aff. tubiba* on *S. mombin*, causing asymmetric exploitative competition. On the other hand, the increased late pollen availability after 0600 hours did not produce a higher visitation rate of honey bees. It is likely that honey bees ignored the pollen sources in such a small scale (several inflorescences) provided by the experiment and

were foraging on other food sources at this time. Thus, foraging trait difference, the fast arrival/ rapid exploitation of honey bees and late arrival/ slow exploitation of stingless bees, is likely to cause the temporal displacement.

The efficiency of the honey bee communication system is well known and explains the bees' ability to recruit many individuals and quickly exploit rich food sources (Dyer 2002). Menezes et al. (2007) observed a similar situation for Africanized honey bees and *Scaptotrigona depilis* Moure foraging on *Schefflera arboricola* (Hayata) Merr. (Araliaceae) in which the first depleted the floral resources before the native species foraged. Evidence of stingless bees' and

other native bees' displacement by honey bees has also been observed by others (Roubik 1978, 1980; Roubik et al. 1986; Goulson 2003).

Although stingless bees species also show complex communication systems (Nieh 2004), honey bees have other advantages related to large colony size and to the ability to forage earlier than many bee species (Schaffer et al. 1979; Horskins and Turner 1999). This "first-come, first-served" behavior of the honey bees thus confers a superior ability to harvest rich floral resources, especially when compared with diurnal native bee species. Given that *S. mombin* is a rich source of pollen, as indicated by the estimated number of pollen loads produced per inflorescence, it is noteworthy that an Africanized honey bee pollen load is similar in size to the large *Melipona* species, but three to ten times more than other stingless bee species (Roubik et al. 1986).

Nevertheless, despite the generalistic foraging habits of the eusocial species, a low overlap in resource use between honey bees and native bees has also been observed in some studies (Pedro and Camargo 1991; Martins et al. 2003). Wilms et al. (1996) observed that, although honey bees were relatively abundant in a tropical rainforest in southeastern Brazil, mass-flowering tree species could provide enough resources for honey bees and stingless bees. Ramalho (2004) also showed, in another tropical rainforest in southeastern Brazil, that honey bees commonly foraged on mass-flowering plants with small flowers, but they did not comprise as large an abundance of foragers as the stingless bees. It is likely that other factors such as resource availability, landscape structure, species composition, and population density have an influence on observed foraging behavior throughout tropical forests.

The long term effects of competition between Africanized honey bee and native bees has not been demonstrated although some studies suggest the occurrence of a silent competition at community level (Roubik 2009; Roubik and Villanueva-Gutiérrez 2009). It has been shown in 17-year period of studies that there was no decline in native bee abundance after African-

ized honey bee invasion in the Neotropics, but honeybees had a major impact at Anacardiaceae and Euphorbiaceae species, causing foraging shift in native bees to floral resources from other taxa (Roubik 2009; Roubik and Villanueva-Gutiérrez 2009).

Several studies of melittophilous flora have listed *S. mombin* as a pollen source for native and honey bees (Sommeijer et al. 1983; Ramalho et al. 1990). Other authors have observed *S. mombin* as a foraging resource only for honey bees (Biesmeijer et al. 1992) and for some genera as *Frieseomelitta* Ihering (Teixeira et al. 2007), *Scaptotrigona* (Marques-Souza et al. 2007), and *Augochlora* Smith (Wcislo et al. 2003). Ramalho et al. (1990) and Sommeijer et al. (1983) also reported *S. mombin* pollen in the pollen loads of some *Melipona* Illiger species. It is thus noteworthy that we observed *Melipona scutellaris* Latreille foraging for pollen in *B. orellana* beside the *S. mombin* flowering trees throughout the 2007–2011 blooming season, with *M. scutellaris* showing a preference for the first. Some workers of *M. scutellaris* were recorded on *S. mombin* flowers only in 2011.

Honey bees have been regarded as effective pollinators of other Anacardiaceae crops such as *A. occidentale* (Freitas and Paxton 1998), *Spondias tuberosa* Arruda (Castro and Barreto 2008) and *M. indica* (Siqueira et al. 2008). In our study, all the bee species touched the stigma frequently and were considered as potential pollinators of *S. mombim*. However, considering the abundance and the ability to visit a large number of flowers, honeybees and *Scaptotrigona aff. tubiba* were regarded as the effective pollinators of *S. mombim*.

A further intriguing feature of the plant–pollinator system of the self-incompatible *S. mombin* studied here is the low rate of fruit set from open pollination in the area. Some Anacardiaceae species commonly suffer from such a low fruit set, including *A. occidentale*, *M. indica*, and *S. tuberosa* (Holanda-Neto et al. 2002; Siqueira et al. 2008; Nadia et al. 2007). In *S. mombin*, fruit set from outcrossing can be favorably selected, as suggested by the lower initial fruit set and fruit survival rate from crosses between clones compared with crosses between

non-clone plants. Thus, the higher fruit set of the hand cross-pollinated flowers from the non-clone treatment compared with those produced by open pollination suggests a deficit in outcrossing at the study site caused by high geitonogamy rates due to the presence of clones. The survival rate was lower in the cross-pollination between non-clones plants compared with open pollination because the initial fruit set was exceedingly high, but the absolute number of produced mature fruits, as well as mature fruit set, was superior.

Further long term studies in areas with a low abundance or absence of honey bees would help to understand this intriguing plant–pollinator system. Additional studies are also necessary to address geitonogamy rates by comparing different regions and areas without clones.

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Les abeilles africanisées pollinisent et collectent prioritairement à toute autre espèce d'abeilles le pollen des fleurs de *Spondias mombin* (Anacardiaceae).

Apis mellifera / réduction du pollen disponible / abeille sans aiguillon / abeille nocturne / pollinisation / Brésil

Afrikanisierte Bienen bestäuben die Blüten von *Spondias mombin* L. (Anacardiaceae) und kommen dabei anderen Bienen zuvor.

Apis mellifera / Pollenreduzierung / Stechellose Bienen / nachtaktive Bienen / Bestäubung / Brasilien

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