Floral resource partitioning by ants and bees in a jambolan *Syzygium jambolanum* (Myrtaceae) agroforestry system in Brazilian Meridional Amazon

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Abstract The fruit production of flowering plants critically depends on the pollination services provided by animals that compete for flower resources. The output of competitive interactions between ants and bees for inflorescences of jambolan *Syzygium jambolanum* (Myrtaceae) in an agroforestry system in Brazilian Meridional Amazonian are an interesting system of investigation due the possibility to control variables experimentally. In 20 *S. jambolanum* individuals we performed 300 treatments in different inflorescences of two strata (upper and lower) as follows: (1) ants exclusion, (2) bees exclusion, and (3) control group where ants and bees could access the inflorescences. There was no difference in the number of inflorescences, volume of nectar and sugar concentration between the strata. Also the visitors considered are distributed equally in the tree's stratum. When bees were prevented from access the inflorescences, ants dominated more inflorescences only in the lower stratum. On the contrary, when ants were excluded, bees visited more inflorescences only in the upper stratum. We conclude that ants prevent the access to bees and vice versa as the result of different ability of resource utilization and foraging strategies. Thus, preventing the access of ants to the floral nectar could increase the level of nectar available to pollinators of *S. jambolanum*, thereby increasing productivity and reducing economic losses.

Introduction

The fruit production of several plants species is limited by the availability of pollination services provided by animals (e.g. Baiardi 1997). For human cultivated plants, conservative estimates indicate that pollination represents annually about $200 billion dollars in benefits (Costanza et al. 1997; Velthuis and Van-Doorn 2006; Gallai et al. 2009). Thus, the decrease in availability of pollinators limits the quantity and quality of fruits (Wallace and Lee 1999; De-Marco and Coelho 2004; Lassen et al. 2011), resulting directly in economic loss (Vianna et al. 2007). Pollen and nectar are important carbohydrates and proteins resource for pollinators although these high energy

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supplies are limited in time and space (Brown et al. 1981; Ramalho et al. 1991; Galen and Geib 2007; Tiple et al. 2009). Bees are the most effective pollinator group on human cultivars and in most plants of different ecosystems (Bawa et al. 1985; Roubik 1989; Pyke 1991; Harder and Barrett 1992; Wäckers et al. 2007). The bee pollination systems are considered a model for several theoretical and empirical studies of competition (Brown et al. 1981; Schaffer et al. 1983; Buys 1987).

Plant–insect interaction commonly presents cases of antagonistic outcomes, which in plant-pollinator systems would be represented by visitors that obtain floral resources without performing pollination (Bronstein et al. 2006; Douglas 2008). The insects involving on nectar thieving are called "cheaters" of this mutualistic relationship (Hoeksema and Bruna 2000; Yu 2001). Nectar thieves may play a role in the stability of communities they belong to, affecting the production of fruits by competition with effective pollinators (Irwin et al. 2001). The ants are a good example of this relationship as they generally establish their colonies in the soil and forage in nearby plants, with high recruitment and resource monopolization (Blüthgen and Fiedler 2004; Blüthgen et al. 2004).

According to Rico-Gray and Oliveira (2007), ants are probably the most dominant insect group on earth and they represent ten to fifteen percent of animal biomass in terrestrial ecosystems. There are many examples on literature of different ant taxa using floral nectar as food resources (Hölldobler and Wilson 1990; Fowler et al. 1991; Davidson et al. 2003; Blüthgen et al. 2004). However, ants are often considered floral cheaters rather than pollinators (Gómez and Zamora 1992; Puterbaugh 1998; Dáttilo et al. 2009). It can be associated to its absence of wings limiting the pollen transport among plants of the same species, a great disadvantage for plants to invest in coevolutionary mechanisms (Hölldobler and Wilson 1990; Rico-Gray 1989). Moreover, most ants have the metapleural gland in the thorax that produces antifungal lipophilic substances (e.g., myrmicacin) which affect the ability of pollen germination or even kill the pollen when in contact to (Beattie 1985).

Here, we investigated the competition between ants and bees for floral nectar in jambolan, *S. jambolanum* (Lam.) DC. (Myrtaceae), in an agroforestry system in Brazilian Meridional Amazonia. We evaluated whether the use of floral resources by one guild negatively interfere the use by the other. We also evaluated if nectar quality (volume and sugar concentration) in different strata may affect this relationship, determining the resource partitioning between ants and bees.

Materials and methods

Study area

This study was conducted in a 13.75 ha jambolan (*S. jambolanum*) plantation in São Nicolau Farm, Cotriguaçu municipality, North of Mato Grosso State, Brazil (9°49′34″S and 58°15′33″W, elev. 254 m). According to Köppen classification, the climate is tropical humid (Am) with mean annual temperature of 24°C, humidity of 85% and mean annual rainfall of 2,300 mm (Veloso et al. 1991; Camargo et al. 2010).

The plantation was installed in 2003 with a 6 × 3 m spacing among individuals, for purposes of reforestation and it is surrounded by Meridional Amazonia Tropical Rain Forest. Field observations were conducted in October 2010, the end of the dry season and during jambolan flowering period.

Species studied

Syzygium jambolanum is a Myrtaceae reaching 8 m tall, which reaches up to 8 m tall and exhibits a dense, broad and highly branched canopy. Originating in India, it is used for ornamental and medical purposes in Brazil, where its fruits are very appreciated and sold at popular fairs (Bragança 1996; Mazzanti et al. 2003; Loguercio et al. 2005). Pollen is the main reward offered to Myrtaceae pollinators, being bees of the family Apidae the most important group among them (Nic Lughadha and Proença 1996; Gressler et al. 2006). In fact, the *S. jambolanum* flowers morphology is typically morphologically adapted to bee pollination (Sakuragui et al. 2011; Torezan-Silingardi 2012). The inflorescences have small white flowers with long stamens that meet in terminal racemes. Flower clusters, 5–6 cm long and wide, forming a trichotomous panicles. The flowers have 1.25 cm wide, 2.5 cm or more in length, and nearly 5 mm in diameter. Shape flowers are conical, light green base, calyx sessile, formed by four-white-rounded-concave petals. The petals, more than 2 mm long are united in a funnel

shape. The threadlike stamens are numerous, white or pinkish and 5 mm long. Pistil with inferior ovary and tiny and white style, 6–7 mm long (Bentham 1863–1878). Visitors and nectar thief could access to nectar chamber formed by united petals. However, only visitors that touch stigmas, located upper floral parts, are able to pollinate *S. jambolanum* (Bentham 1863–1878; Sakuragui et al. 2011). Flowering period of *S. jambolanum* is between September and November, when nectar and pollen are mainly collected by bees (Câmara et al. 2004; Sobral et al. 2010).

Data collection

To evaluate stratification in the nectar availability, 20 individuals of *S. jambolanum* were randomly selected on a monoculture of more than 500 individuals. In each plant we counted the number of flower, buds, fruits and petiole scars in two inflorescences, one at a height <1.8 m and other at a height greater than 1.8 m and taller than 3.2 m. The stratification was observed once that upper 1.8 m the almost all flowers were receiving light. In some species, the light can influence the nectar production (e.g. Boose 1997; Cawoy et al. 2008). The difference on quality of resource, in this case on sugar concentration, can be determinant to create niche segregation. So, in order to determine if there is difference on nectar quality produced on both strata, total sugars in nectar were evaluated in 10 inflorescences per plant, five at a height <1.8 m and five at a height between 1.8 and 3.2 m tall. All inflorescences had at least six open flowers. To exclude bees and ants, we covered 10 inflorescences in each tree with paper bags and put non-toxic grease in the inflorescence petiole. The visitor access to the inflorescences was prevented 3 h prior the beginning of the measurements. Biased on naturalistic observations, this time period was considered enough to the ant or a bee discover and dominate the available resource. We measured the volume of nectar (by graduates micro-capillary) and the total concentration of sugars in nectar (by portable refractometer RT-280 Instrutherm®) in six flowers per inflorescence.

To verify if bees and ants are mutually exclusive, we realized reciprocal removal experiments. For this, we divide the canopy into two strata: upper (≥1.8 m) and lower (≤1.8 m) and chose 300 inflorescences, 150 in each stratum. All inflorescences selected had at least six open flowers on the day of the experiment.

Subsequently, we randomly separated the inflorescences in three groups of 50 inflorescences per stratum and established the following treatments: (1) isolation and removal of ants visitors by applying non-toxic grease on the petiole of the inflorescence, allowing access to bees, (2) removal and isolation of bees, covering the inflorescences with paper bags but allowing access to ants by the petiole, and (3) control group where the manipulation of inflorescence consisted only of removal of visitors, as done in the treatment 1 and 2, but without isolating the inflorescence of subsequent visitors. Each treatment was followed by an observation period of about 2 min, during which all of bee visits and/or ants were recorded. Also, we conduct additional observations in order to determine eventual flower visitors that can interfere on the results.

Data analysis

We used the *T* Test to verify the differences in mean of volume, total sugar content of nectar, and the number of buttons and flowers between upper and lower strata of *S. jambolanum*. Additionally, we used maximum likelihood χ^2 tests (*G* tests) to compare the frequency of occurrence of ants and bees in the three treatments of the different strata of *S. jambolanum*. We used the program SYSTAT 10.0.0 (Wilkinson 1998) in all analyses.

Results

The number of summed reproductive structures as flowers, buds, fruits and petiole scars per inflorescence did not differ between the strata of *S. jambolanum*, averaging 8.75 ± 6.49 in the upper stratum and 11.7 ± 10.43 in the lower stratum ($T = -1.073$, $DF = 8.31$, $P = 0.291$). Additionally, the volume of nectar produced by flowers also did not differ between the strata of *S. jambolanum*, averaging 3.86 ± 2.06 (mL) in the upper stratum and 3.9 ± 1.75 (mL) in the lower stratum ($T = -0.054$, $DF = 37.1$, $P = 0.957$), as well as the concentration of sugars found in nectar, with a mean of 25.29 ± 10.3 (%) in the upper stratum and 25.47 ± 13.82 (%) in the lower stratum ($T = -0.033$, $DF = 35.4$, $P = 0.974$).

In the control group of experimental inflorescences we did not observe replacements between the visitors

(ants for bees and vice versa). The most abundant and frequent ant on the studied *S. jambolanum* plantation was an undetermined *Pheidole* (sp1) (Formicidae: Myrmicinae). This ant species clearly nests on soil once we could determine the foraging trail from soil to the branches in all cases. In some rare exceptions, some workers of *Cephalotes* sp1 (Formicidae: Myrmicinae) and *Pseudomyrmex* sp1 (Formicidae: Pseudomyrmecinae) co-occurred with the workers of *Pheidole* sp1. All these three ant species are small enough to do not reach the stigma of the flowers. So, all the three ant species are clearly nectar thieves and was grouped here as "ants". We also observe Hesperid butterflies visiting and probably accessing the floral nectar. However, as they are large enough, the butterflies do not (or just fortuity) touch stigma as well, being also nectar thieves. However, as they occurs in low abundance in the agroforestry, do not collect pollen, and do not shows aggressive behavior, but flee upon encounter with ants (pers. obs.) this group of nectar thieves was not considered as biological relevant in this system and in the study area. The only possible pollinators observed among the insect visiting *S. jambolanum* flowers during the experimental period were bees, since all of them has the correct size and behavior to touch on stigma of the flower during the pollen and nectar collection. In fact, several bee was observed visiting *S. jambolanum* flowers, particularly *Scaptotrigonas* sp., *Trigona* sps., *Tetrgoniscas* sp. and *Apis mellifera*. They are all grouped as "bees" because of its potentiality as pollinators.

In natural conditions (control group), the frequency of ants on inflorescences did not differ between of the upper and lower strata of *S. jambolanum* ($G = 0.026$, $DF = 1.000$, $P = 0.872$). The observed bees belong to four different species. Despite of intrinsic different behaviors, we assume that all species form a natural group of pollinators being more similar in foraging and resource exploitation than among bees and ants. When bees were prevented to access the inflorescences in the upper stratum, there was no increase in the ant visitation frequency of that stratum when compared with the control group ($G = 0.040$, $DF = 1,000$, $P = 0.842$). However, when bees were prevented to access the inflorescences in the lower stratum, ants visited 29% more inflorescences ($G = 7.4$; $DF = 1,000$; $P = 0.007$) (Fig. 1).

In the control group the bees did not differ in the frequency of visitation between inflorescences of the
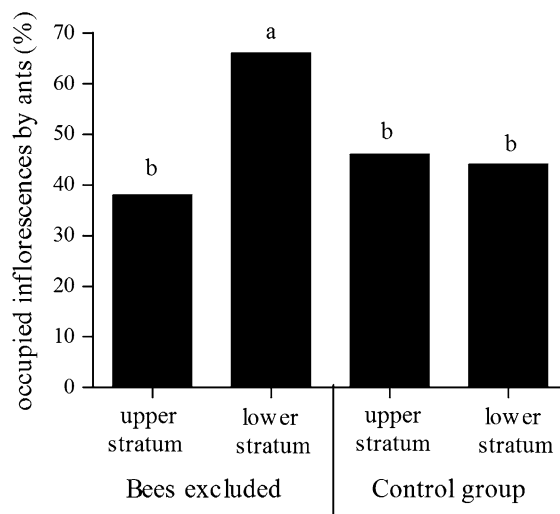

Fig. 1 Frequency of occupied inflorescences by ants in the upper and lower stratum of jambolan *S. jambolanum* (Myrtaceae) in two treatments: bees-excluded (bees were prevented from having access to the inflorescences) and control group (bees had access to the inflorescences). *Different letters* indicate that the results are statistically different ($n = 50$ for each treatment)

upper and lower strata of *S. jambolanum* ($G = 0.010$; $DF = 1.000$; $P = 0.920$). When we prevent the access of ants to inflorescences located in the upper stratum, bees visited 30% more inflorescences ($G = 9.716$; $DF = 1.000$; $P = 0.002$). However, when we remove the ants from inflorescences in the lower stratum there was no increase in the frequency of bee visitation in this stratum ($G = 0.012$; $DF = 1.000$; $P = 0.912$) (Fig. 2).

Discussion

Several studies have shown that ants can compete with bees by floral nectar, reducing the availability of the resource and/or aggressively preventing the access of bees (Johnson and Hubbell 1974; Hubbell and Johnson 1978; Schaffer et al. 1983; Nagamitsu and Inoue 1997; Galen and Geib 2007). However, this study differs from several others by showing that both, bees and ants, avoid agonistic encounters by generating a pattern of vertical stratification on its competitive effort. In this case we can assume that there is competition for inflorescences just in a specific stratum to each group. This pattern may represent an important way of resource partitioning, contributing to
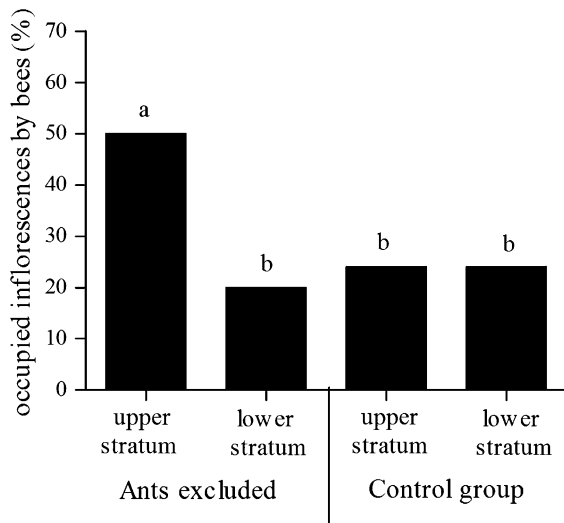
Fig. 2 Frequency of occupied inflorescences by bees in the upper and lower stratum of jambolan *S. jambolanum* (Myrtaceae) in two treatments: ant-excluded (ants were prevented from having access to the inflorescences) and control group (ants had access to the inflorescences). *Different letters* indicate that the results are statistically different ($n = 50$ for each treatment)

the structure and maintenance of their populations over time (Wiens 1976; Bawa et al. 1985; Itino and Yamane 1995; Oliveira and Campos 1996; Brühl et al. 1998). Although we have not shown a natural structuration in bee and ant occupancy at the studied scale, it is possible that another structuration occurs between different heights of the canopy of *S. jambolanum*, since different foraging strategies may influence the floral nectaries occupation and domination (Nagamitsu and Inoue 1997; Koptur and Truong 1998).

Once there is no variation in nectar production or quality between upper and lower flowers, it is expected that, at the beginning of the activities of ants and bees, the workers tend to dominate the major number of the more accessible flowers to each group (Nagamitsu and Inoue 1997; Koptur and Truong 1998). However, we did not observe differences in the proportions of ants or bees occupying upper or lower inflorescences in unmanipulated (control) trees. Ants and bees start their activities apparently at the same time (very early in the morning). So, why is there no segregation on the natural occupancy of inflorescences? It can be explained by a neutral process of occupancy of inflorescences. We observed that the flowers do not open synchronically. In this case, both ants, and bees forage during mornings on all tree inflorescences for flowers producing nectar. Due

to the asynchrony, the dominance of an inflorescence was determined just by its encounter during foraging of few workers of both, ants or bees. Additionally, on the control group, once the inflorescence was occupied, there were no (observed) replacements between ants and bees along the day, probably due to a constant nectar replacement. It produced a non-segregated pattern on inflorescences occupancy on a single tree.

The results of the interference competition could be demonstrated because all the experiments were conducted after the opening and dominance of the major part of inflorescences. When ants were excluded from inflorescences of the two strata, the frequency of bee visitation increased only in the upper stratum. It was possibly due to some specific behavior related to flight pattern that defines the ability of location of food and hence in learning (Jean-Prost 1985; Frankie and Coville 1979; Menzel et al. 2005). But, when the bees are excluded from the upper and lower strata, there is an increase in ants' frequency only in the lower one. One possible explanation is that ants would maximize the gain of energetic liquid, through a trade-off among the cost of searching for food near the nest, competitive interactions and nutritional benefits (optimal foraging) (MacArthur and Pianka 1966). In fact, in both cases, the dominance was observed just on the most accessible part of tree to each competitor.

This study suggests that interactions between ants and bees imply on direct interference between them, but also suggests that this relationship is asymmetrically modulated by the different localization and ability of resource utilization. In this case, we suggest that the presence of ants can significantly decrease the production per tree, since the ants are not good pollinators (Gómez and Zamora 1992; Puterbaugh 1998; Dáttilo et al. 2009). Thus, beyond of losses inflicted on agricultural and forestry systems due to accented herbivory (Mariconi 1970; Della Lucia 1993), ants cause reduction in gene flow and affect the access of effective pollinators to *S. jambolanum*. We can not infer that limiting the access of ants to the floral nectar fruit production would be increased. However, the control of ants could increase the production at the lower stratum, which can increase the ease of harvest. Therefore, it could increase the level of nectar available to pollinators, thereby increasing productivity and reducing economic losses. We suggest future studies to quantify the success in fruit production in plantations with and without access of ants to different tree species.

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