



RESEARCH ARTICLE - ANTS

Effects of ants on pollinator performance in a distylous pericarpial nectary-bearing Rubiaceae in Brazilian Cerrado

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Abstract

Besides the effectiveness of floral visitors, to better understand pollination systems is necessary to consider the role of predators. Ants are ubiquitous on the vegetation, especially on plants bearing extrafloral (EFNs) and pericarpial nectaries (PNs). Both EFNs and PNs reward ants which in turn provide to plants effective protection against herbivores. However, ants can also repel pollinators and cause an indirect cost for the plant partner, although the role of ants on pollinators' performance has rarely been assessed in Neotropics, mainly on PN-bearing plants. Here, our main aim was, through an experimental field study in terms of ant's presence versus absence, to test the hypothesis that ants dissuade floral visitors by decreasing the time spent during visits on the PN-bearing *Declieuxia fruticosa*. Additionally, we recorded floral phenology, and quantified and qualified floral visits. We showed that bees were the most frequent pollinators and the presence of ants dissuades them. In ant presence, pollinators were on average 30% faster than without ants. Since *D. fruticosa* produces fruits mainly after cross-pollination, the role of ants may be profitable to plants as they induce pollinators to do shorter visits and search for other flowers in conspecific plants. Therefore, pollinators avoid stay at longer on plants with ants in order to avoid attacks, which may contribute to plant outcrossing. However, whether positive or negative the effects of ants on *D. fruticosa* reproduction are, they remain to be studied.

Introduction

Around 87.5% of angiosperms are pollinated by animals, of which insects are the main groups (Ollerton et al., 2011). Lepidoptera (~140.000 species), Coleoptera (~80.000 species), Hymenoptera (~70.000 species), and Diptera (~55.000 species) represent the most diverse pollinating insect orders (Ollerton, 2017). Nevertheless, their effectiveness as plant partners, i.e. contributing for increasing plant reproductive success (fruit/seed set), varies taxonomic and spatio-temporally (Ollerton, 2017). In order to assess the relative performance of different groups of pollinators, three components are usually evaluated: (i) the abundance of the animal in a community; (ii) the propensity for that animal to touch anthers, carry pollen, and

contact stigmas; and (iii) whether or not the animal will move to a flower of the same species and the distance it travels to do so (Herrera, 1987; Rodriguez-Rodriguez et al., 2013). By analyzing these components, it has long been suggested that the most dominant pollinating taxon is Apidae, since bees can be relatively large, hairy and show the kinds of behaviors, see below, that make them most effective pollinators than that from its and other insect orders (Ollerton, 2017). However, to better understand plant-pollinator systems, multitrophic interactions must also be considered (Assunção et al., 2014). For instance, recent studies suggest that pollinating insects such as bees can avoid or evade from plants where their predators (e.g. ants and spiders) are present and thus triggering a negative cascading ecosystem effect (Antiqueira & Romero, 2016; Huey &



Nieh, 2017). Thereby, besides pollinator effectiveness, predators can also play a central role in plant-pollinator systems because they may change pollinator behavior and affect plant reproduction.

Ants are particularly abundant on the vegetation from Brazilian Cerrado, especially on plants bearing extrafloral nectaries (EFNs; Rico-Gray & Oliveira, 2007; Del-Claro et al., 2016; Calixto et al., 2018). EFNs are secretory glands not related to pollination (Koptur, 2005), which can be found in vegetative as well as in reproductive structures (Rico-Gray & Oliveira, 2007). When EFNs are present in fruits and derived from persistent floral nectaries, which continue secreting nectar after flower senescence and corolla abscission, they are called pericarpial nectaries (PNs; Del-Claro et al., 2013; Sanz-Veiga et al., 2017). Both EFNs and PNs attract ants which feed on them and in counterpart generally provide to plants effective protection against herbivores (Rico-Gray & Oliveira, 2007; Nascimento & Del-Claro, 2010). However, some studies have shown that ants can repel pollinators and cause an indirect cost for the plant partner (Willmer & Stone, 1997; Junker et al., 2007; Assunção et al., 2014).

For instance, it was found that the presence of ants on *Cassia alata* L. (Fabaceae) decreased the frequency of pollinators' floral visits; and on *Wedelia trilobata* A. St.-Hil. (Asteraceae) and *Diospyros durionoides* Bakh. (Ebenaceae) pollinators remained longer at flowers in which ants were removed (Junker et al., 2007). Furthermore, it was reported that aggressive *Ectatomma* ants cause avoidance of bees (e.g. *Trigona* sp.) on *Heteropterys pteropetala* A. Juss. (Malpighiaceae) (Assunção et al., 2014). On the other hand, it has been shown that ants can deter only less effective pollinators and then increasing plant reproductive success (González et al., 2013). Thus, the role of ants on pollinating systems is context-dependent, with positive or negative effects depending on whether they deter all floral visitors or a subset of them (González et al., 2013). Nonetheless, the role of ants on pollinator performance and plant reproductive success has rarely been assessed in Neotropics, especially on PN-bearing plants (but see Assunção et al., 2014; Sanz-Veiga et al., 2017).

Declieuxia fruticosa (Wild. ex Ruiz and Pav.) Kuntze is a distylous and PN-bearing Rubiaceae of Cerrado (Fig 1).

This plant species presents two types of floral morphologies, that includes individuals producing flowers with long style and short stamens (pin or long-styled flowers), or plants producing flower with short style and long stamens (thrum or short-styled flowers) (Hamilton, 1990; Barrett, 1992). The morphological variation between distylous groups is related to the reproductive system, in which the maintenance of different floral morphologies (pin or thrum) is related to a heteromorphic self-incompatibility system. This system determines that only pollinator-mediated crosses between plants with different floral morphologies to set fruits and seeds (Barrett & Richards, 1990).

Declieuxia fruticosa is pollinated only by insects (Matias et al., 2016), and recently ants were found visiting PNs during the flowering (Sousa-Lopes, pers. obs.). In order to better understand the system and evaluate the effect of ants on floral visitors, our main aims were: (i) to describe the floral phenology of *D. fruticosa* and associated ants; (ii) to quantify the frequency and qualify the floral visitors (effectiveness: effective or eventual pollinators and robbers, see below) on the two morphologies of *D. fruticosa* (pin and thrum); and (iii), through an experimental field study in terms of ant presence versus absence, to test the hypothesis that ants dissuade floral visitors by decreasing the time spent during visits.

Material and Methods

Study area and plant species

Fieldwork was conducted from February to March 2016 in a Brazilian Cerrado area of the ecological reserve of the Clube Caça e Pesca Itororó de Uberlândia (CCPIU), Minas Gerais state (18°59'S, 48°17'W), Brazil. The reserve has ~270 ha and is dominated by grasses and shrubs, but trees are also present, ranging from 2 to 8 m tall (more details in Ferreira & Torezan-Silingardi, 2013). The climate of the region is markedly seasonal, characterized by two periods: a warm and rainy (October to April), which may concentrate 75% of annual rainfall, and another less warm and dry (May to September) (Laboratory of Climatology, Federal University of Uberlândia - UFU, see Vilela et al., 2014).

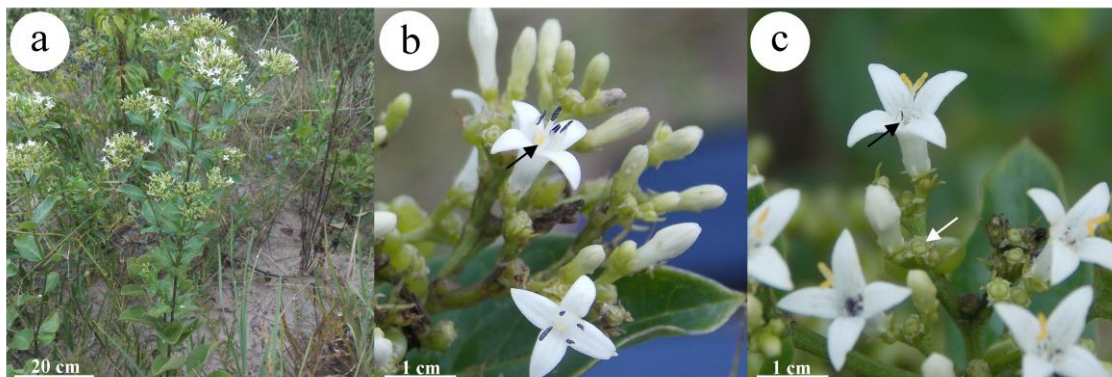


Fig 1. *Declieuxia fruticosa* (Rubiaceae) in a cerrado area from CCPIU, Uberlândia, Minas Gerais state, Brazil: a) plant architecture, b) thrum individual; see the purple anthers and the arrow showing the stigma, and c) pin individual; see the bifurcated stigma, the black arrow showing one of anthers, and the white arrow showing a pericarpial nectary.

Declieuxia fruticosa is a shrub commonly found in cerrado areas in Minas Gerais state (Araújo et al., 2002), ranging from 7 to 150 cm tall (Delprete 2010, Fig 1). The species has aggregate distribution, and in a plot of 1,800 m² of the CCPIU reserve we found 124 individuals, of which 63 had thrum flowers and 61 had pin flowers (isopleth: close ratio of 1:1; Chi-square test with Yates correction = 0.008, $p = 0.93$).

Floral phenology and resources

We randomly chose 42 *D. fruticosa* individuals (21 with pin and 21 with thrum flowers) of similar size and at least 3 m apart, and inspected them from 06:00 am to 06:00 pm during five days. Then we evaluated the time of anthesis, period of pollen availability and stigmatic receptivity. To investigate the stigmatic receptivity, all flowers were previously bagged with voile bags until the time of analysis. After 10 minutes of flower opening, stigmatic receptivity tests were conducted with a 30 minutes interval on different flowers ($n = 20$). The surface of the stigma was carefully inserted into a clear tube with 3% of hydrogen peroxide and if there was blistering, the stigma was considered receptive (Dafni & Maués, 1998). Pollen availability was determined every 30 minutes by touching the anthers on a black surface ($n = 20$). When there was pollen, the grains fell on the surface and became evident, following Assunção et al. (2014).

Floral visitors and ant experiment

We randomly selected another 10 individuals (five pin and five thrum) of *D. fruticosa* with similar characteristics (height, number of branches, approximate percentage of buds, flowers and fruits). Then, we inspected them from 06:00 am to 06:00 pm, two individuals per day in sessions lasting 25 minutes per plant and with resting of 10 minutes between sessions ($n = 12$ sessions per individual plant per day). Individuals of *D. fruticosa* were arbitrarily divided into two groups: ants present (control) and ants absent (treatment). In the treatment, we applied a layer of atoxic resin (Tanglefoot™) around the plant stem 20 cm from the ground to prevent ants to access the plants. Also, we removed neighborhood plants and branches that could serve as bridge. In the control, we applied Tanglefoot only in one side of the plant stem, thus allowing ants to access the plant (following Bächtold et al., 2017). During observations we recorded absolute frequency, time spent visiting, time of day and behavior of floral visitors in both control and treatment plants. We recorded floral visitors and ants, and when possible, we collected specimens on non-experimental plants to avoid interference. Voucher specimens were deposited in the Behavioral Ecology and Interactions Laboratory (LECI) at the UFU.

The behavior of floral visitors and ants were observed *ad libitum* (sensu Altmann, 1974). For the categorization of floral visitors (effective pollinators, eventual pollinators or robbers), frequency and visitation behaviors were evaluated, especially whether there was contact with the reproductive

parts of the flower (adapted from Coelho & Barbosa, 2003). Therefore, the effective pollinators were considered to be the insects that usually touched the anther and the stigma and moved to another flower of the same plant species. The eventual pollinators were the insects that sometimes touched the anther and/or the stigma and moved to another flower of the same plant species. The robber only exploited the resources without touching the plant reproductive parts or transfer pollen (adapted from Alves-dos-Santos et al., 2016).

Data analysis

The frequency of each floral visitor is presented in a circular network where plant morphologies (pin and thrum) are the nodes and pollinators' floral visits are grouped on them. To analyze the relationship between the number of visits of floral visitors, as well as the time spent by floral visitors on flowers, and the abundance of ants on plants, we used a Multivariate Analysis of Variance (MANOVA). For that, we used the average number of visits per plant per hour and the time spent in the visit per plant per hour as our dependent variables; and the average of ants abundance per plant per hour of control plants as our predictor variable. After that, we conducted analyzes separately to identify which dependent variable that contributed to the significant global effect.

To compare the time spent during visits per plant per hour between the control and treatment, we conducted a Student t-test. All analyses were made in R software 3.6.1 (R Development Core Team, 2015) with 5% of probability. We checked normality and variance of the data with Shapiro-Wilk and Levene test respectively.

Results

Floral phenology and resources

The time with the highest number of plants in anthesis, 81% ($n = 34$), occurred at 09:00 am. Only two individuals presented open flowers at 07:00 am, three at 09:30 am and another three at 10:00 am. Pollen was available at 06:30 am ($n = 4$), when the flowers were not yet fully opened, but pollen grains were already visible in the anthers. Most of the plants presented pollen availability between 08:00 am ($n = 7$) and 09:00 am ($n = 9$), while the latter occurred at 09:30 am ($n = 1$). The end of pollen availability occurred at 1:00 pm, when it was no longer possible to observe pollen grains as they were already removed. The stigma receptivity always occurred at 09:00 am, but about 2:00 to 2:30 pm. The flowers of both morphs lasted about four hours.

Floral visitors and ant experiment

We found thirty-eight morphospecies of floral visitors belonging to the orders Lepidoptera ($n=15$), Hymenoptera ($n=13$), Diptera ($n=05$), Coleoptera ($n=02$), Hemiptera ($n=02$) and Orthoptera ($n=01$) (Table 1, Fig S1). Hymenopterans accounted for 70% of the total number of visits and 62% of

their floral visitors interacting with both plant morphotypes (Fig 2, Table 1). Thirteen species were considered pollinators (effective or occasional, Table 1), eight hymenopterans and

five lepidopterans. *Apis mellifera* Linnaeus, 1758 and *Trigona spinipes* (Fabricius, 1793) were the pollinators most frequent in this system, accounting for 897 visits (~49%).

Table 1. Number of records, followed by relative frequency (%) and the functional classification of insect species associated to thrum and pin flowers of *Declieuxia fruticosa* in a cerrado area of Uberlândia, Minas Gerais state, Brazil.

Floral visitor Order/Species	Morphotypes of <i>D. fruticosa</i>			Activity ²
	Thrum	Pin	Total	
Hymenoptera				
<i>Apis mellifera</i> Linnaeus, 1758	550(46.81) ¹	164(25.27)	714(39.14)	EFP
<i>Trigona spinipes</i> (Fabricius, 1793)	97(8.25)	86(13.25)	183(10.03)	EFP
<i>Oxaea flavescens</i> Klug, 1807	78(6.64)	68(10.48)	146(8.00)	EVP
<i>Pepsis</i> sp.	72(6.13)	45(35.58)	117(6.41)	EFP
<i>Campsomeris</i> sp.	14(1.19)	64(6.93)	78(4.28)	EVP
Hymenoptera sp. 1	0(0)	21(3.23)	21(1.15)	ROB
<i>Bembix</i> sp.	0(0)	06(0.92)	06(0.33)	ROB
<i>Augochloropsis</i> sp.	03(0.25)	03(0.46)	06(0.33)	EVP
<i>Augochlora</i> sp.	03(0.25)	03(0.46)	06(0.33)	EVP
Hymenoptera sp. 2	05(0.42)	0(0)	05(0.27)	ROB
<i>Melipona</i> sp.	04(0.34)	01(0.15)	05(0.27)	EVP
<i>Brachygastra lecheguana</i> (Latreille, 1824)	0(0)	03(0.46)	03(0.16)	ROB
<i>Pachymenes</i> sp.	02(0.17)	0(0)	02(0.11)	ROB
Lepidoptera				
<i>Urbanus proteus</i> (Linnaeus, 1758)	49(4.17)	32(4.93)	81(4.44)	EFP
Arctiinae sp. 1	06(0.51)	10(1.54)	16(0.88)	EVP
<i>Heraclides</i> sp.	05(0.42)	11(1.69)	16(0.88)	EVP
Hesperiidae sp. 2	05(0.42)	10(1.54)	15(0.82)	EVP
<i>Mimoniades</i> sp.	13(1.11)	0(0)	13(0.71)	ROB
<i>Stalactis phlegia</i> (Cramer, 1779)	0(0)	08(1.23)	08(0.44)	ROB
<i>Hylephila</i> sp.	08(0.68)	0(0)	08(0.44)	ROB
<i>Macroglossum</i> sp.	0(0)	05(0.77)	05(0.27)	ROB
<i>Diaphania</i> sp.	04(0.34)	0(0)	04(0.22)	ROB
<i>Calycopis</i> sp.	03(0.25)	01(0.15)	04(0.22)	EVP
<i>Heliopetes omrina</i> (Butler, 1870)	02(0.17)	0(0)	02(0.11)	ROB
Arctiinae sp. 2	0(0)	02(0.31)	02(0.11)	ROB
<i>Syngamia florella</i> (Stoll, 1781)	02(0.17)	0(0)	02(0.11)	ROB
<i>Junonia</i> sp.	0(0)	01(0.15)	02(0.11)	ROB
Hesperiidae sp. 1	01(0.08)	0(0)	01(0.05)	ROB
Diptera				
<i>Chrysomya megacephala</i> (Fabricius, 1974)	166(14.13)	67(10.32)	233(12.78)	ROB
<i>Sarcophagidae</i> sp.	72(6.13)	14(2.16)	86(4.71)	ROB
<i>Archytas</i> sp. 2	02(0.17)	16(2.46)	18(0.99)	ROB
<i>Archytas</i> sp. 1	05(0.42)	0(0)	05(0.27)	ROB
<i>Syrphidae</i> sp.	0(0)	04(0.62)	04(0.22)	ROB
Coleoptera				
Curculionidae sp.	0(0)	04(0.62)	04(0.22)	ROB
Coccinellidae sp.	01(0.08)	0(0)	01(0.05)	ROB
Hemiptera				
Coreidae sp.	01(0.08)	0(0)	01(0.05)	ROB
<i>Apiomerus</i> sp.	01(0.08)	0(0)	01(0.05)	ROB
Orthoptera				
Orthoptera sp.	01(0.08)	0(0)	01(0.05)	HER
Total	1175(64.42)	649(35.58)	1824(100)	-

¹Number of records (relative frequency in %); ²HER - herbivore, EFP - effective pollinator, EVP - eventual pollinator and ROB - robber.

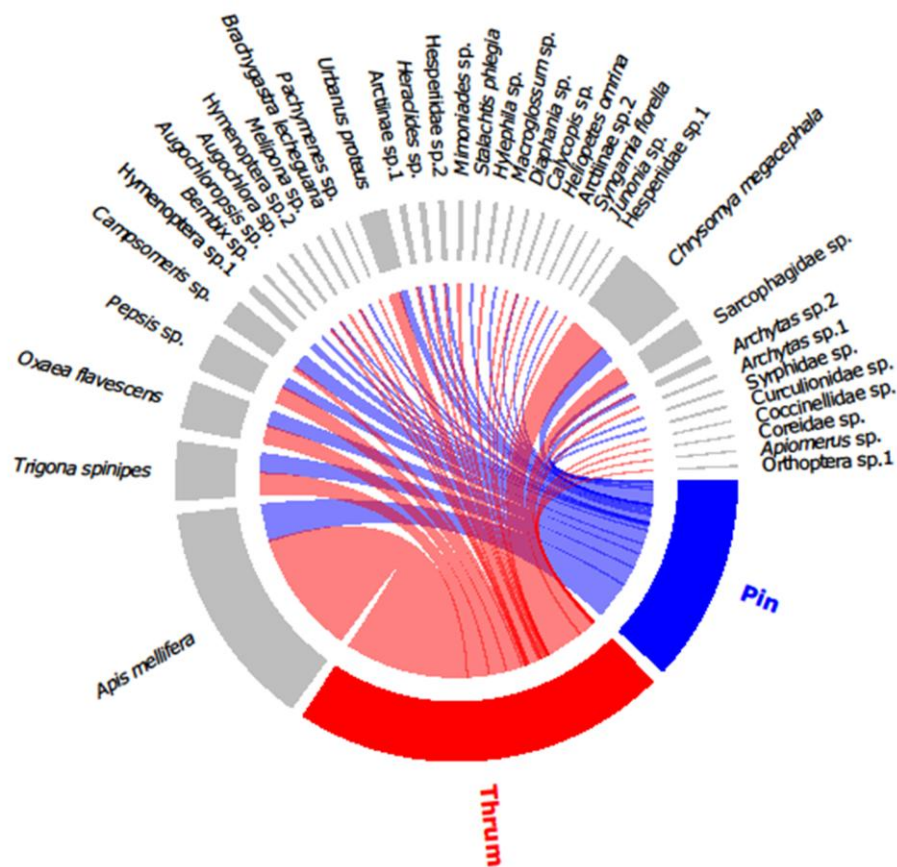


Fig 2. Interactions network between the two morphotypes of *Declieuxia fruticosa*, thrum (red) and pin (blue), and their floral visitors. Note that few species, for example, *Apis mellifera* interact with a disproportionate higher frequency with the plant.

We recorded 169 visits from four ant species patrolling PNs of *D. fruticosa* (Table 2). *Ectatomma brunneum* and *Camponotus crassus* accounted for 86% of ant visits. Individuals of *E. brunneum*, were seen attacking two individuals of *A. mellifera* that visited flowers near PNs.

Floral visitors had two activity peaks, one at 11 am and another at 2 pm in both control and treatment (Fig 3a). The average number of visits on treatment plants was greater than in control plants. The abundance of ants had peak activity at 12 and 13 pm and then started to decrease. We observed that our global multivariate test between the number of visits and the time spent by visit and ant abundance was significant (MANOVA: Pillai = 0.658, $p < 0.01$). From specific models

Table 2. Absolute (and relative, %) frequency of ants visiting pericarpial nectaries from thrum and pin individuals of *Declieuxia fruticosa* in Brazilian Cerrado.

Ant	Thrum	Pin
<i>Brachymyrmex</i> sp.	12(10)	0
<i>Camponotus crassus</i> Mayr, 1862	32(27)	44(85)
<i>Camponotus</i> sp.	09(8)	02(4)
<i>Ectatoma brunneum</i> Smith, 1858	64(55)	06(11)
Total	117	52

for each variable, we found that both, time spent by visit ($F = 16.61$, $p < 0.01$; Fig 3b) and the number of visits ($F = 7.164$, $p < 0.05$; Fig 3c), were significant.

We found that the amount of time spent during visits per plant per hour differed significantly between the control and treatment ($t = 2.271$, $df = 23$, $p < 0.05$; Fig 4). Floral visitors stayed longer on plants without ants (8.14 ± 1.83 s) than on plants with ants (6.30 ± 2.16 s).

Discussion

Our study corroborates the hypothesis that ant presence dissuades floral visitors by decreasing the number and time spent during visits. Since *D. fruticosa* produces fruits mainly after cross-pollination (Matias et al., 2016), the role of ants can be beneficial to the plants as they induce pollinators to do shorter visits and search for other flowers or other plants.

Aguirre et al. (2018) also found that ant presence on flowers of *Vigna luteola* (Jacq.) Benth. (Fabaceae) changes the behavior of floral visitors with potential beneficial effects to the host plant. In this system authors observed that the main plant pollinator, the bee *Megachile* (Pseudocentron) sp., spent less time in flowers than non-pollinators. They also noted that sometimes ants scare away the pollinator, but in these cases the latter had already performed the pollination service.

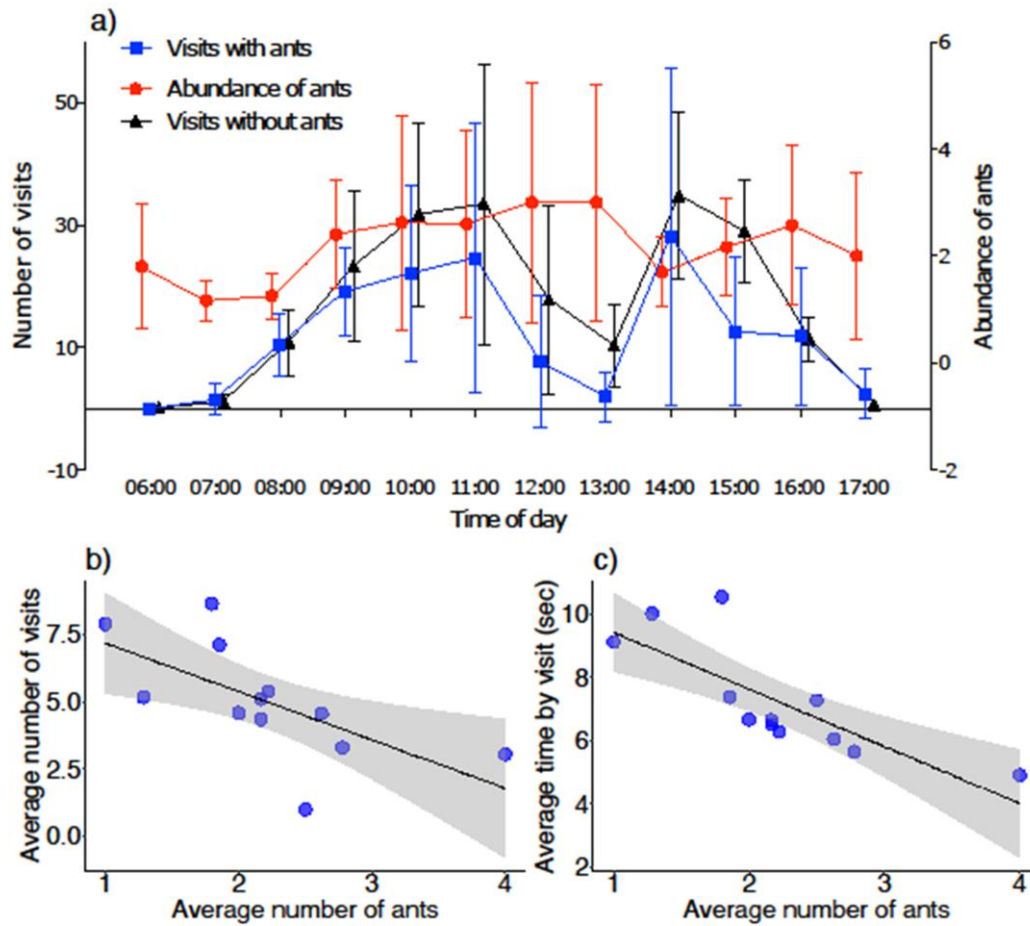


Fig 3. a) Average number of visits by floral visitors (blue) and abundance of ants (red) per plant per hour in control (with ants), and average number of visits by floral visitors (black) in treatment (without ants). Points and bars represent mean \pm SD. b) Relationship between average number of visits by floral visitors and abundance of ants per plant per hour in control. c) Relationship between the average time spent per visit by floral visitors and abundance of ants per plant per hour in control plants.

So, authors concluded that ants have a dual function in this system: they protect the plant against potential herbivores and filter flowers against potential nectar thieves, since non-pollinator insects spend a lot of time on flowers and then ants can attack and chase away them. Studying *Psychotria limonensis* K. Krause (Rubiaceae) in Panama, Altshuler (1999) also found that the aggressive ants *Ectatomma* contributed to higher pollination success. Ant presence allowed higher relocation frequency of winged pollinators and also the rate of flower visitation, although ants were detrimental to fruit removal by avian frugivores (Altshuler, 1999; see also Dáttilo et al., 2016). In contrast, in *C. alata* as well as in *Turnera velutina* Benth. (Turneraceae), ant presence decreased the frequency of visits by pollinators and it was suggested that ants can negatively affect pollination (Junker et al. 2007; Villamil et al., 2018). Here, we have shown that ants visiting *D. fruticosa* PNs may interfere with the pollination services, and we suggest the result of this action is conditioned by the ant and pollinator species present. In case pollinators have to move faster from one flower to the other due to ants on pericarpial nectaries, their presence may increase plant fruit-set.

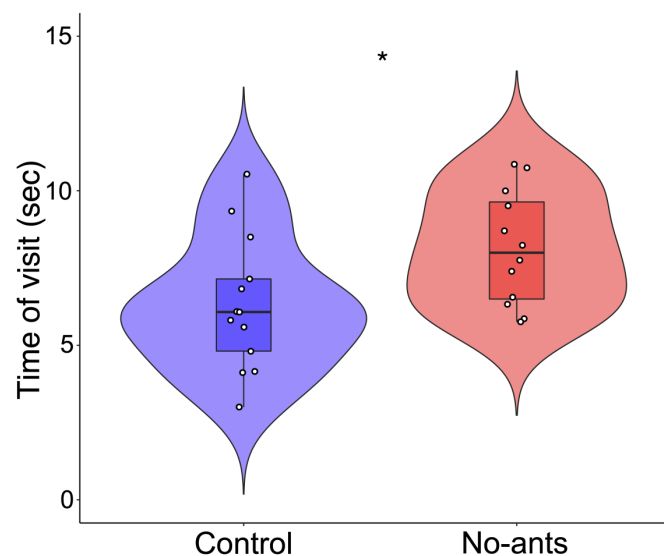


Fig 4. Average time spent per visit per plant per hour by floral visitors in the control (ants present) and treatment (ants excluded) on *Declieuxia fruticosa*. Figures show a violin plot represented by a boxplot and a rotated kernel density (probability density) plot. * $t = 2.271$, $df = 23$, $p < 0.05$.

This situation is similar to that observed on *Adenocalymma bracteatum* (Cham.) DC. (Bignoniaceae) in which robbers decrease floral nectar and force pollinators to increase the number of floral visits to find enough food resources (Almeida-Soares et al., 2010).

Ants may also be acting as fruit protectors of *D. fruticosa* (see Calixto et al., 2018; Sanz-Veiga et al., 2017), since some Rubiaceae of the Cerrado have an intense rate of parasitism (Del-Claro et al., 2013). However, studying *Palicourea rigida* Kunth. in Brazilian Cerrado, it was found that ants did not protect fruits against seed-parasitic wasps (Del-Claro et al., 2013). Furthermore, ants may have a deleterious effect on fruit dispersal through decreasing the rates of visitation and fruit removal since they repel potential visually oriented fruit dispersers (Dáttilo et al., 2016). Nonetheless, questions on the role of ants as plant bodyguards were not addressed here and then further studies on this subject will be welcome to better understand the system.

Most effective floral visitors of *D. fruticosa* had larger frequency of visits than eventual pollinators and robbers. As expected, the main floral visitors were bees, especially *A. mellifera* and *T. spinipes*. These bees had high abundance, were propense to touch anthers, carry pollen, and contact stigmas, and they also were seen moving pollen from one flower to another of the same species. So, although we did not quantify the seed set, based on the characteristics above mentioned it is possible that bees have high effectiveness for *D. fruticosa* (Herrera, 1987; Rodriguez-Rodriguez et al., 2013; Ollerton, 2017). Indeed, bees are the most outstanding pollinators in different ecosystems, accounting up to 80% of pollination services (see Carreck & Williams, 1998; Potts et al., 2010; Clemente et al., 2012). Thus, we reinforce the importance of bees for the maintenance of pollination services in Rubiaceae from Brazilian Cerrado.

Therefore, we recorded the floral phenology of *D. fruticosa*, its floral visitors and associated ants. It was highlighted that the presence of ants near to flowers changes pollinator behavior through an decrease in the number of visits and a reduction in the time spent during visits. Then it is a clear and direct evidence that pollinators reduce foraging time per flower on plants with ants in order to avoid attacks, which were also recorded here (but see Junker et al., 2007; Assunção et al., 2014). However, whether positive or negative the effects of ants on *D. fruticosa* reproduction are, they remain to be studied, although it is possible that ants can contribute to plant outcrossing since bees may move more among flowers and plant individuals in ant presence.

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List of Supplementary Figures



Fig S 1. Floral visitors of *Declieuxia fruticosa*. (1) *Apis mellifera*, (2) Hymenoptera sp. 1, (3) *Campsomeris* sp. and (4) *Trigona spinipes*.

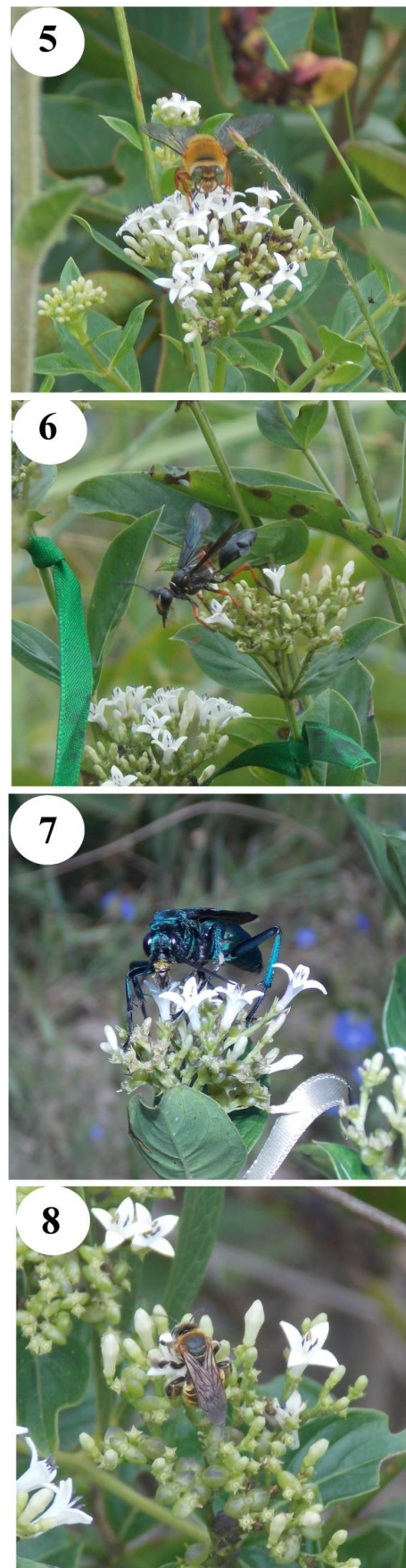


Fig S 2. Floral visitors of *Declieuxia fruticosa*. (5) *Oxaea flavescens*, (6) Hymenoptera sp. 2, (7) *Pepsis* sp. and (8) *Melipona* sp.

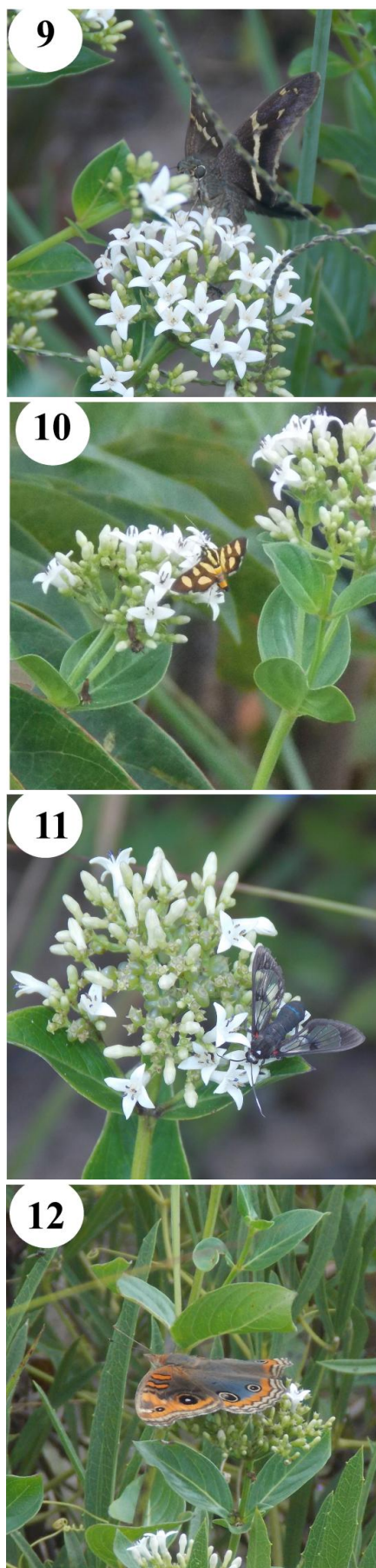


Fig S 3. Floral visitors of *Declieuxia fruticosa*. (9) *Urbanus proteus*, (10) *Syngamia florella*, (11) *Arctiinae* sp. 1 and (12) *Junonia* sp.



Fig S 4. Floral visitors of *Declieuxia fruticosa*. (13) *Hesperidae* sp. 1, (14) *Hesperidae* sp. 2, (15) *Calycopis* sp. and (16) *Macroglossum* sp.



Fig S 5. Floral visitors of *Declieuxia fruticosa*. (17) *Mimoniades* sp., (18) *Heliopete omrina*, (19) *Diaphania* sp. and (20) *Heraclides* sp.



Fig S 6. Floral visitors of *Declieuxia fruticosa*. (21) *Stalactis phlegia*, (22) *Arctiinae* sp. 2, (23) *Hylephila* sp. and (24) *Archytas* sp. 1.



Fig S 7. Floral visitors of *Declieuxia fruticosa*. (25) *Archytas* sp. 2, (26) *Sarcophagidae* sp., (27) *Chrysomya megacephala* and (28) *Coccinelidae* sp.

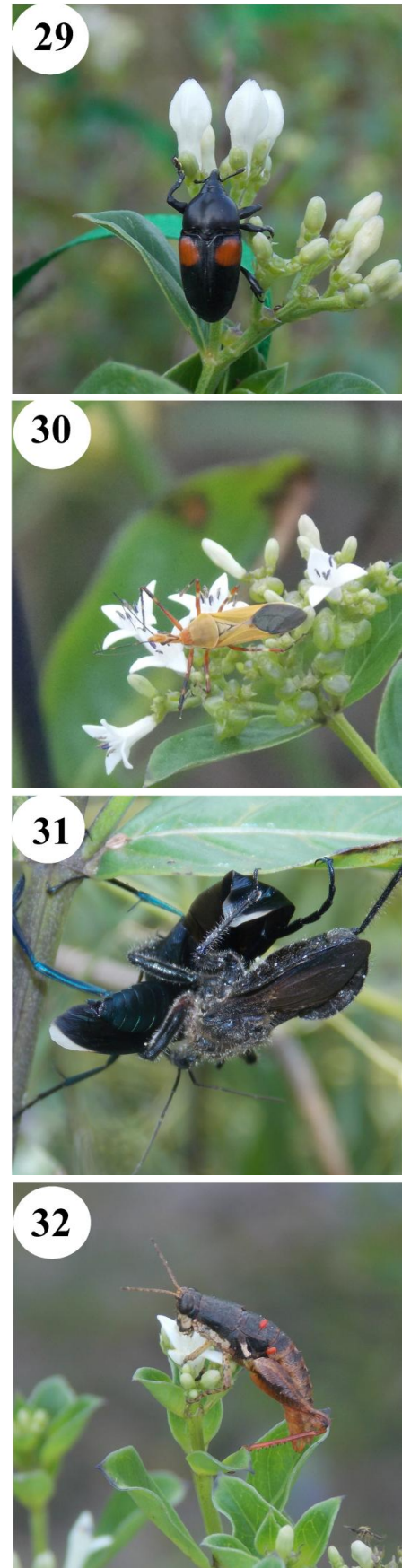


Fig S 8. Floral visitors of *Declieuxia fruticosa*. (29) *Curculionidae* sp., (30) *Coreidae* sp., (31) *Apiomerus* sp. preying on the effective floral visitor *Pepsis* sp., below a leaf after capturing it in the flower of *D. fruticosa* and (32) *Orthoptera* sp.



Fig S 9. Ants associated to pericarpial nectaries of *Declieuxia fruticosa*. (1) *Ectatomma brunneum* and (2) *Camponotus* sp. Note *E. brunneum* visiting pericarpial nectaries near a flower.