



Higher flower number in *Jatropha mutabilis* (Euphorbiaceae) increases the frequency of floral visitors in the Caatinga dry forest

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Abstract

The spatial distribution of floral resources directly affects the foraging pattern of pollinators. In addition, plant–pollinator interactions are linked to a great diversity of visual, chemical, and morphological signals, which interfere with plant reproduction. Here, we aimed to understand how flower distribution of *Jatropha mutabilis* (Euphorbiaceae) affects the foraging behavior of its floral visitors. We hypothesized that an increase in the (i) number of flowering individuals, (ii) total number of open flowers, or (iii) floral display (number of open flowers/inflorescences) increases the number of floral visitors. The study was carried out in a Caatinga dry forest in Pernambuco, Brazil. The number of flowering individuals/plot, the total number of open flowers/plot, and the floral display/inflorescence/plot were counted in 37 plots. Those parameters were also analyzed separately for male and female flowers since the species is monoecious. We documented that the number of floral visits was positively correlated with the number of flowering individuals and the total number of open flowers/plot but did not correlate with floral display/inflorescence. We observed interactive effect of the number of open flowers/plot and floral display affecting visitors' frequency, which was higher with both: increased number of open flowers/plot and lower floral display. Floral sex did not correlate with the analyzed parameters. Our findings show that plant–floral visitor interactions are sensitive to changes in the intraspecific number of open flowers/plot, independently of flower sex. High flower production scattered among individuals, as in *Jatropha mutabilis*, increases the chances of pollination and maintenance of plant species and floral visitors, which is especially important in seasonally dry tropical forests, such as the Caatinga dry forest.

Keywords Floral display · Flower distribution · Monoecy · Plant–animal interactions · Pollination · Seasonally dry tropical forests

Introduction

The distribution of flowers in the environment strongly influences the foraging behavior of floral visitors (e.g., Klinkhamer et al. 2001; Grindeland et al. 2005; Dauber et al. 2010; Pyke 2016). In nature, resources are unevenly distributed in space and time (e.g., Wiens 1976). Therefore, the foraging pattern of floral visitors depends on the amount of available resources and also on how floral resources are distributed both among individuals, which is called attractiveness or floral display, and in the population, which represents

the local density of flowers (Hodges 1995; Klinkhamer et al. 2001; Grindeland et al. 2005). Increases in the density of plant individuals, associated with an increase in resource supply, such as an increase in nectar production, tend to positively affect the attractiveness of floral visitors (e.g., Grindeland et al. 2005; Dauber et al. 2010; Pyke 2016).

The interactions between flowers and their visitors involve a great diversity of chemical and visual signals, which interfere in the reproduction of most angiosperms (e.g., Faegri and Pijl 1979; Endress 1994; Proctor et al. 1996; Ollerton et al. 2011; Willmer 2011) and in the maintenance of many species of floral visitors (Faegri and Pijl 1979; Willmer 2011). A variety of floral traits, such as color, shape, size, floral resource, and odor, are responsible for influencing visitor behavior (e.g., Morawetz and Spaethe 2012; Farré-Armengol et al. 2013; Shrestha et al. 2013; Yan et al. 2016; Pellegrino et al. 2017), and consequently the efficiency of pollen flow in each visit (Essenberg 2012). Phenotypic

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manipulation experiments reinforce the idea that floral traits result from selection mediated by pollinators (Schiestl and Johnson 2013) to optimize the reproductive success of plants (e.g., Sletvold et al. 2010). These experiments showed, for example, that the rate of visits to flowers was impaired by a decrease in floral size (Zhao and Wang 2015), removal of the lip, and modification of the color of the labellum in orchids (Pellegrino et al. 2017), and decrease in nectar volume and concentration (Keasar et al. 2008).

However, studies on floral display and local flower attractiveness focusing on monoecious or dioecious species are scarce (for example, Eckhart 1991; Shykoff and Buchelli 1995; Vaughton and Ramsey 1998). Similarly, there are few studies with this approach in tropical regions (Feinsinger et al. 1991; Vaughton and Ramsey 1998), and there is no record of studies for arid or semiarid ecosystems. In tropical ecosystems, biotic pollination prevails among plants (e.g., Gottsberger 1985; Machado and Lopes 2002; Ollerton et al. 2011), and animals are responsible for pollinating almost 90% of the angiosperms (Bawa 1980; Ollerton et al. 2011).

The Caatinga Phytogeographic Domain is a Seasonally Dry Tropical Forest (SDTF) restricted to Brazil and represents the largest semiarid region in South America, occupying 912,529 km² (Silva et al. 2017). The Caatinga dry forest is located in northeastern Brazil, bordering the Atlantic forest domain to the east and the Cerrado to the west and south. The seasonality and rainfall distribution, associated with elevated temperatures and highly variable edaphic conditions, generate a diverse spectrum of Caatinga phytophysionomies (e.g., Moro et al. 2014, 2015). These range from open areas with shrubby and herbaceous vegetation, such as inselbergs, to areas where tree species dominate in species richness and abundance, such as arboreal Caatinga (sensu Graeff 2015). In total, around 28.6 million people inhabit the Caatinga (Silva et al. 2017), exerting anthropic pressures such as subsistence farming, livestock farming, and chronic extraction of timber and non-timber forest products (e.g., Leal et al. 2014; Ribeiro et al. 2015; Arnan et al. 2018).

The Caatinga dry forest seasonality (including precipitation and soil water availability) and the intensity of chronic anthropogenic disturbances alter the supply of floral resources (e.g., Machado et al. 1997; Barbosa et al. 2003; Martorell and Peters 2005; Amorim et al. 2009; Ureta and Martorell 2009; Silva et al. 2020). Therefore, studies on pollination ecology in the Caatinga dry forest are essential for designing ecosystem management projects (e.g., Machado and Lopes 2004). We aimed to understand how flower distribution of *Jatropha mutabilis*, a monoecious species occurring widely in the Caatinga dry forest, interferes with the foraging behavior of its floral visitors. We hypothesized that an increase in the (i) number of flowering individuals, (ii) number of open flowers, or (iii) floral display (number of open flowers/day in five inflorescences of five individuals/

plot) disproportionately increases the number of flower visits. It is expected that the greater the number of flowering individuals and open flowers per plot, and open flowers per inflorescence, the greater the number of visits received by *J. mutabilis* flowers in the Caatinga dry forest. Additionally, the hypotheses were tested separately for female and male flowers. We expected that male flowers, being more numerous and having, in addition to nectar, pollen (which could function as a secondary resource), will receive more visits than female flowers.

Materials and methods

Study area

This study was carried out in Catimbau National Park, state of Pernambuco, Brazil (8° 24' 00"–8° 36' 35" S, 37° 09' 30"–37° 14' 40" W), which spans an area of 622.94 km². This focal landscape spreads over low-altitude plateaus with a predominance of sandy soils plus relictual outcrops. The climate is semiarid, hot, and dry: BSh (Köppen 1948), with a mean annual temperature of 25 °C (Silva et al. 2017), and annual rainfall (highly seasonal) ranging between 450 and 1,200 mm (Andrade et al. 2017). The park was officially designated as a strictly protected area in 2002, as the core area of the UNESCO Caatinga Biosphere Reserve. However, the Catimbau National Park is still home to many rural and indigenous inhabitants, who extract firewood and non-timber forest products, hunt wildlife, practice family agriculture and extensive livestock husbandry, and exert chronic disturbances at different intensities in several regions of the park (e.g., Arnan et al. 2018). Land use throughout the study area was expanded by 704% between 2000 and 2014, due to the increasing human activity (Freire 2015).

Study species

Jatropha mutabilis is a native and endemic plant species of Brazil, occurring widely in the Caatinga phytogeographic domain (Galindo 1985; Flora do Brasil 2022). It has a shrubby habit, red open/dish flowers (Fig. 1), monoecious sexual system (Webster 1994a, b), self-pollination by geitonogamy (Santos et al. 2005), and the fruit is a dry schizocarp (Webster 1994a, b). Female and male flowers are similar in size (♀ 25–28 mm in diameter and ♂ 26–27 mm in diameter), petal color, and both produce nectar as a floral resource (Santos et al. 2005). On average, female flowers secrete nectar with 35 mg of sugar per flower and 133 µL of volume, while male flowers secrete nectar with 18 mg of sugar per flower and 73 µL of volume (Neves et al. 2011). The nectar volume reaches its maximum value at 10 h, and soon after it decreases with an increase in the sugar concentration (Neves

Fig. 1 Male (A) and female (B) flowers of *Jatropha mutabilis* (Pohl) Baill. (Euphorbiaceae) in the Caatinga dry forest at the Catimbau National Park, Buíque, Pernambuco, Brazil



et al. 2011). Anthesis begins at 4:00 a.m. for both sexes and about 1:30 h later, female flowers have receptive stigmas and male flowers have open anthers. In the Caatinga dry forest, *J. mutabilis* is pollinated by the specialist bees *Eulaema nigrita* and *Xylocopa grisescens*, in addition to the hummingbirds *Chlorostilbon aureoventris*, *Amazilia* sp. and *Chrysolampis mosquitos* (effective pollinators), the bees *Apis mellifera* and *Trigona spinipes*, and the wasp *Polybia paulista* (occasional pollinators) (Santos et al. 2005). The species exhibits a continuous flowering pattern in the Caatinga dry forest, without a flowering peak for male flowers (which are significantly more numerous than females, as detailed just below), and a peak of female flowers (defined by more inflorescences with an open female flower) in August and September (Santos et al. 2005). The first flower to open on each inflorescence is always a female one, which lasts about 36 h. Then, the morning after the senescence of the female flower, male flowers open (male flowers last about 12 h). The following day, a female flower opens for another 36 h, repeating the described sequence. In a single inflorescence, a maximum of one female flower opens per day, while up to eight male flowers can be found open each day (Santos et al. 2005).

Flower distribution

To verify the effects of the number of flowering individuals of *Jatropha mutabilis* on the frequency of floral visitors, we marked 37 plots, experimentally, with 30 m² (5 m × 6 m) each, all of them in the same soil type in Catimbau National Park. Plots were at least 30 m apart. No other plant species were observed flowering during the study period in the marked plots. We counted the total number of flowering individuals and open flowers for each plot. To calculate the floral display (number of open flowers per inflorescence), five inflorescences from five different individuals in each plot were randomly chosen and marked and had the number of open flowers per day counted; female and male flowers

were also counted separately. Inflorescences with a larger display were considered as those presenting a higher number of open flowers per day.

Frequency of flower visitors

Floral visitors were observed in the 37 plots during flowering, distributed between 05:00 h and 16:30 h (within the floral anthesis time sensu Santos et al. 2005). The daily observations of each plot were performed during the morning and afternoon and repeated at different times of the day, following a protocol adapted from Garibaldi et al. (2020). Each day, floral visitors were observed in three plots (two flowering individuals per plot), with a 30-min stay in each plot between 5:00 a.m. and 8:30 a.m., 9:30 a.m. and 14:30 h, and 15:30–16:30 h. Thus, the first plot was observed for 30 min, then the second plot was observed for 30 min, and finally the third. Observations in the three plots were repeated throughout the day, totaling 7 h of observations per day. Observations in the 37 plots were made on consecutive days. We counted the number of open flowers in focal individuals during the observations and registered the number and time of visits for each 30-min observation interval in each of the 37 plots.

Data analyses

First, to verify the existence of groups of floral visitors related to floral sex, we applied a non-metric multidimensional scaling (NMDS) and a species composition analysis (ANOSIM) based on Bray–Curtis dissimilarity matrices using the *vegan* package (Oksanen et al. 2020) in R (R Core Team 2020). Then, we tested the correlation between the variables, and as we did not observe a correlation, all were kept in the study. To check the difference in the number of visits between male and female flowers in relation to the observation time, we applied the *t.test* function within the

car package in R version 3.3.1 (R Core Team 2016). Generalized linear models (GLMs) (Sokal and Rohlf 1995) were applied to verify the isolated and combined effects of the number of flowering individuals and open flowers per plot, and open flowers per inflorescence on the number of visits. Additionally, this analysis was performed separately for male ($N=20$, randomly selected from the sample) and female flowers ($N=20$, also randomly selected). The selection of best-supported models was based on the corrected Akaike information criterion (AICc), which reduces biases associated with multiple tests, variable collinearity, and small sample sizes (Burnham and Anderson 2002). We initially built full models, with the best-supported models selected based on their respective AICc weights, which inform the probability of a given model diverging from chance. We selected models with AICc differences lower than two ($\Delta\text{AICc} < 2$). Predictors were considered most important if retained in the best-supported models that did not contain only the intercept. Model selection was performed using the *dredge* function in the *MuMIn* package (Burnham and Anderson 2002) in R (R Core Team 2020).

Results

Flower distribution of *Jatropha mutabilis*

Jatropha mutabilis presented a total of 376 flowering individuals and 510 open flowers in the 37 plots (132 female and 378 male), with an average of 10.15 ± 6.03 flowering individuals per plot and 13.68 ± 7.25 open flowers per plot. Considering the inflorescences, an average of 4.35 ± 3.10 open flowers per inflorescence was observed. Thus, male flowers are produced at a rate up to four times higher than female flowers in each individual of *J. mutabilis* and this relationship was ten times greater when considering the whole plot. In addition, *J. mutabilis* presented temporal separation in the appearance of female and male flowers ($N=173$ inflorescences), as detailed above (Study Species), with female flowers always opening first in each inflorescence. Only four of the 173 analyzed inflorescences had male and female flowers open simultaneously.

Frequency of flower visitors

In total, 105 open flowers (20 female and 85 male) were observed for visitors in the focal individuals studied in the 37 plots. Each plot had an average of 2.83 ± 0.75 open flowers/day in the two focal individuals. We observed 130 visits to the 105 observed open flowers of *J. mutabilis* (20 female and 85 male) during the entire observation period. The number of visits per flower varied from 1 to 5, and per plot varied from 1 to 20. Male flowers received 107 visits,

corresponding to approximately 82.3% of the total, while the female flowers received 23 visits (17.7%) ($t = -2.40$; $P = 0.02$; Fig. 2A). Although anthesis started at the same time (about 4:00 a.m.) in flowers of both sexes and flowers were fully open at about 5:30 a.m. (on separate days for each sex, as detailed above), visits occurred mainly between 9:30 and 10:00 h for female flowers, and between 7:30 h and 08:00 h for male ones, with no difference in the number of visits between male and female flowers/hour ($t = -1.73$; $P = 0.09$; Fig. 2B, C). During the observation period of 16:00–16:30 h, none of the observed flowers received visits regardless of floral sex (Fig. 2). Male flowers received visits from the bee *Trigona spinipes*, the hummingbird *Chlorostilbon aureoventris*, the butterfly *Phoebis sennae*, and a species of Diptera. The female flowers were visited by the bee *Trigona spinipes*, the hummingbird *Anopetia gounellei*, the butterflies *Phoebis sennae*, *Euptoieta hegesia meridiana*, and *Eurema elathea*, and by a species of Saturniidae (Lepidoptera) (Table 1). The most frequent visitor in male flowers was the bee *Trigona spinipes*, while in female flowers it was the butterfly *Phoebis sennae* (Fig. 2B, C). Based on the ordination analysis, there are some differences in the floral visitor community between female and male flowers, with a clear formation of two groups (ANOSIM: $R = 0.615$, $P < 0.002$; Fig. 3).

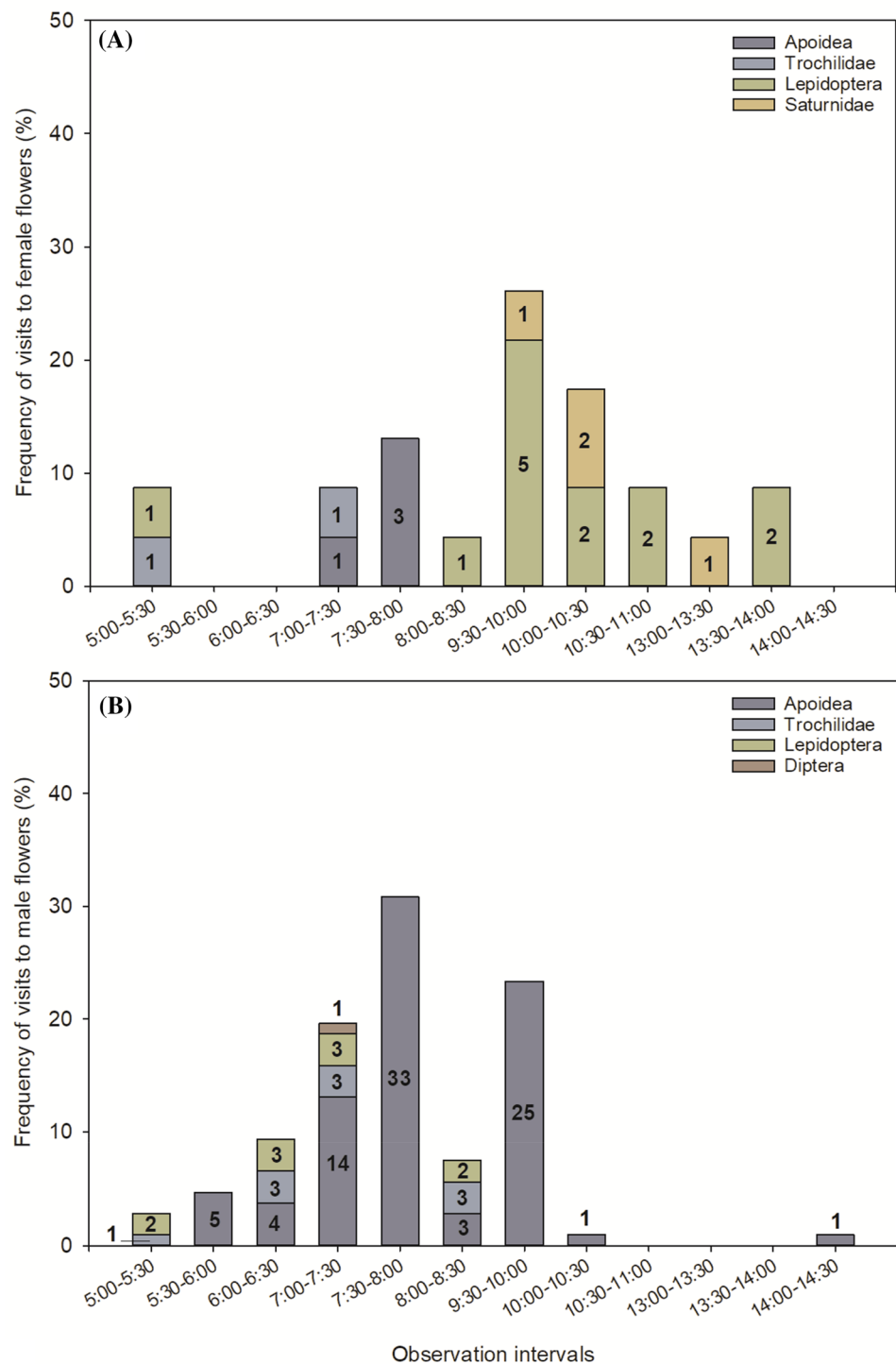
Relationship between resource distribution and number of floral visits

In isolation, the selected models showed that the number of visits was positively correlated with the number of flowering individuals per plot and the number of open flowers per plot, without correlation with floral display/inflorescence (Table 2), corroborating the first two proposed hypotheses. In addition, we observed a combined effect of the number of open flowers per plot with the number of open flowers per inflorescence, where the visiting rate was higher with an increase in the number of open flowers per plot and smaller floral display/inflorescence (i.e., number of open flowers per inflorescence) (Fig. 4). Both female and male flowers, in isolation and combination, showed no change in the rate of floral visits in relation to the number of flowering individuals and open flowers per plot, and floral display/inflorescence (Tables 2 and 3).

Discussion

Our results reinforce the idea that floral visitors of *J. mutabilis* can adapt their foraging behavior to variations in the availability of floral resources in space and time, despite the greater production of male flowers in relation to female ones. Specifically, the local distribution of open flowers (number

Fig. 2 Frequency of visits to female (A) and male (B) flowers of *Jatropha mutabilis* (Pohl) Baill. (Euphorbiaceae) in the Caatinga dry forest at the Catimbau National Park, Buíque, Pernambuco, Brazil. The numbers in each section of the bar represent the number of visits from each floral visitor group



of flowering individuals and open flowers per plot) is more attractive to floral visitors than the floral display/inflorescence, corroborating two of our three proposed hypotheses. Contrary to what we expected, flower sex did not influence the total number of floral visits, neither when analyzing the local distribution of open flowers/individual/plot nor in relation to floral display (open flowers/inflorescence), although

the floral visitor guilds presented some differences between the floral sexes. The observed pattern is discussed in light of the trade-off between high floral attractiveness and geitonogamy in plant species.

The higher production of male flowers compared to female flowers in *J. mutabilis* is similar to that found in other monoecious species (e.g., Piratelli et al. 1998; Lenzi

Table 1 Floral visitors and number of visits to male and female flowers of *Jatropha mutabilis* (Pohl) Baill. (Euphorbiaceae) in a Caatinga dry forest area at the Catimbau National Park, Buíque, Pernambuco, Brazil

	Male flower	Female flower
Apoidae		
<i>Trigona spinipes</i>	X (86)	X (4)
Trochilidae		
<i>Chlorostilbon aureoventris</i>	X (10)	
<i>Anopetia gounellei</i>		X (2)
Lepidoptera		
<i>Phoebis sennae</i>	X (10)	X (9)
<i>Euptoieta hegesia meridiana</i>		X (3)
<i>Eurema elathea</i>		X (1)
Saturniidae		
Sp.1		X (4)
Diptera		
Sp.1	X (1)	

The interaction between flower type and pollinator is indicated by “X”. The number of visits is between parentheses

et al. 2005; Mercadante-Simões et al. 2006). This strategy is a consequence of sexual selection, which can thus favor male floral attractiveness and the visiting rate (Bawa 1980; Delph and Lively 1992; Delph et al. 1996; Huang et al. 2006), therefore promoting greater pollen dispersion (Stanton et al. 1986; Mayer and Charlesworth 1991; Willson 1994). Male flowers, which are more numerous and produce

both pollen and nectar, seem to be more attractive to floral visitors, especially bees, when compared to female flowers (Huang et al. 2006). Furthermore, the yellow coloration of the anthers contrasting with the red coloration of the petals of the male flowers, as observed in *J. mutabilis*, could contribute to a higher attractiveness of bees (Ibarra et al. 2014). All this together may explain the higher number of visits by the bee *Trigona spinipes* to male flowers, despite female flowers opening before and having more nectar per flower (as discussed below). However, considering the total number of floral visits (by all visitors), we did not observe differences by floral sex, as discussed below.

Indeed, plant species may separate their sex functions spatially and temporally (e.g., de Jong and Klinkhamer 2005). In the case of *J. mutabilis*, the inflorescences last an average of 20 days, and the first flower to open is always a female (this study and Santos et al. 2005). The remaining buds within the same inflorescence open successively, alternating female and male flowers on different days (Santos et al. 2005). In this temporal organization of flower opening, the inflorescences are functionally male or female (Santos et al. 2005). The temporal separation of female and male functions is believed to have evolved to minimize self-pollination within the same flower or plant species (Bertin 1993). In addition, our results indicate that there is also a small temporal separation (about 2 h) between visits, between visits to male flowers of one inflorescence and female flowers of other inflorescences. Male flowers receive visits before female flowers, facilitating the collection and subsequent

Fig. 3 Non-metric multidimensional scaling ordination based on the species of floral visitors of *Jatropha mutabilis* (Pohl) Baill. (Euphorbiaceae) in the Caatinga dry forest at the Catimbau National Park, Buíque, Pernambuco, Brazil

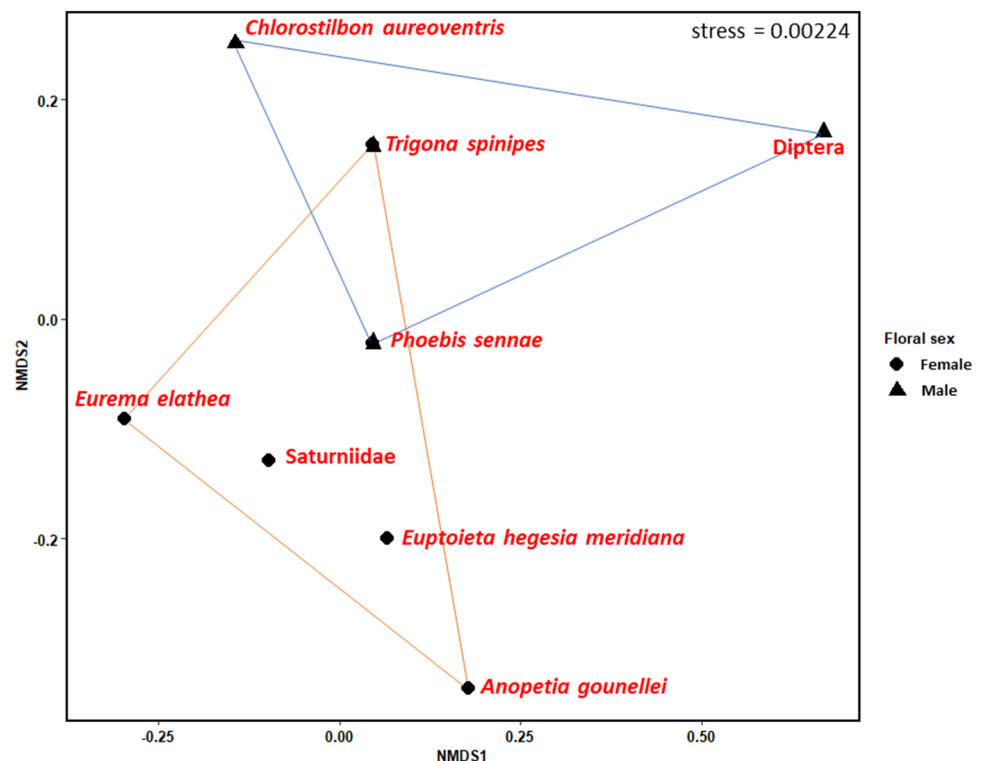
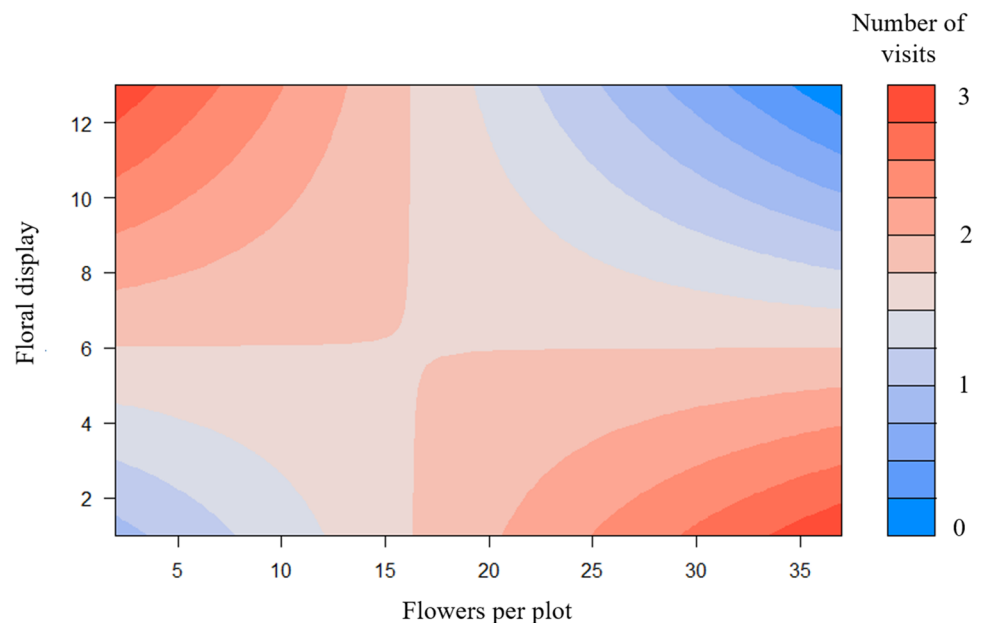


Table 2 Isolated and combined effects of the number of flowering individuals and open flowers per plot, and floral display (number of open flowers per inflorescence) on the number of visits to flowers of *Jatropha mutabilis* (Pohl) Baill. (Euphorbiaceae) in a Caatinga dry forest area, at the Catimbau National Park, Buíque, Pernambuco, Brazil

	Number of visits	Estimates	Error	<i>t</i>	<i>P</i>
Total number of visits					
Number of flowering individuals/plot	+	−0.112	0.058	−1.92	<0.0001
Number of open flowers/plot	+	0.152	0.038	3.91	<0.0001
Floral display		−0.034	0.074	−0.46	0.64
Number of flowering individuals/plot: floral display		−0.001	0.002	−0.72	0.48
Number of open flowers/plot: floral display	X	0.041	0.008	4.75	<0.0001
Visits to female flowers					
Number of flowering individuals/plot		−0.066	0.231	−0.28	0.77
Number of open flowers/plot		−0.070	0.115	−0.61	0.55
Floral display		−0.253	0.235	−1.07	0.30
Number of flowering individuals/plot: floral display		0.005	0.008	0.64	0.53
Number of open flowers/plot: floral display		−0.024	0.072	−0.33	0.74
Visits to male flowers					
Number of flowering individuals per plot		−0.116	0.058	−0.17	0.89
Number of open flowers per plot		0.152	0.038	1.93	0.73
Floral display		−0.034	0.074	−1.05	0.36
Number of flowering individuals/plot: floral display		−0.001	0.001	1.97	0.46
Number of open flowers/plot: floral display		0.045	0.008	−1.37	0.85

Fig. 4 Combined effect of the number of open flowers per plot and floral display (open flowers/inflorescence) in the total number of visits to flowers of *Jatropha mutabilis* (Pohl) Baill. (Euphorbiaceae) in the Caatinga dry forest at the Catimbau National Park, Buíque, Pernambuco, Brazil



deposit of pollen by floral visitors. Thus, the temporal separation in male and female functions and temporal separation of visits in *J. mutabilis*, in association with the behavior of the floral visitors, may positively contribute to the pollen flow and the reproductive success of the species.

Our results revealed that female and male flowers presented some differences between floral visitor guilds [but see also floral visitors (effective and occasional pollinators and thieves) registered by Santos et al. 2005)], with *Trigona*

spinipes and *Phoebis sennae* visiting and pollinating female and male flowers. However, the number of flowering individuals and open flowers per plot seem to favor the visits of *T. spinipes*. This bee can be an important pollinator of *J. mutabilis* due to its habit of intensely foraging female and male flowers in the early hours of the morning. In addition to the distribution of flowers, climatic factors, such as the temperature of the local environment, can influence the period of activity of *T. spinipes*. Indeed, periods of high

Table 3 Isolated and combined effects of the number of flowering individuals per plot (NInd), number of open flowers per plot (NFls), and floral display (number of open flowers per inflorescence)

Response variable	Selected variables	df	AICc	Δ AICc	Weight	R^2
Total number of visits	NInd + NFls	7	288.3	0.00	0.708	0.56
	NFls + NFls: DisF	8	290.1	1.78	0.291	0.51
Visits to female flowers	—	5	59.0	0.00	0.369	0.54
	NFls + DisF	3	59.5	0.51	0.286	0.31
Visits to male flowers	NInd	3	48.6	0.00	0.550	0.68
	—	4	39.3	0.76	0.382	0.61

Best-supported models (Δ AICc < 2)

temperature resulted in an increase in the number of visits of this bee (Soares et al. 2019). From 9 to 14:30 h, the female flowers receive visits only from butterflies, which is compatible with the peak volume and concentration of nectar produced (Santos et al. 2005); while male flowers continued to receive few visits only from *T. spinipes* due to the depletion of pollen supply and lower volume of nectar. Nevertheless, the flower sex did not change the total number of floral visits. This pattern can be explained by the fact that female and male flowers have similar morphologies, such as color, shape, size, and number of petals. Also, although male flowers are significantly more numerous, female flowers present more nectar (each female flower secretes practically twice the volume secreted by a male flower, according to Neves et al. 2011).

Despite the high attractiveness, plant species with more flowering individuals than others may provide fewer resources by inflorescence and/or flower (Cruden 2000; Stone and Jenkins 2007). The cost to produce nectar and pollen together (as is the case of male flowers of *J. mutabilis*) is high (Cruden 2000) and a change in nectar production, such as volume and sugar concentration, can decrease the rate of visits to nearby flowers or even create an avoidance to revisiting (Wang et al. 2013; Zhang et al. 2014; Pyke 2016), explaining the interactive effect of a higher visitation rate in plots with higher density of open flowers/individual and a smaller floral display (open flowers/inflorescence). In addition, in plants with a greater number of open flowers per inflorescence, floral visitors tend to travel more to nearby flowers in sequence and thus transfer pollen between flowers of the same individual (Klinkhamer et al. 1989; Mitchell et al. 2004). Even in monocious plant species with a self-compatible system, such as *J. mutabilis*, the high number of visits to flowers of the same inflorescence belonging to the same individual could contribute to geitonogamy (Robertson 1992; Klinkhamer et al. 1997; Karron and Mitchell 2012). In these species, geitonogamy can reduce female and male fitness resulting in low fruit set and lower genetic variability of seeds (Husband and Schaemske 1996; Hao et al. 2012). If

(DisF) on the total visits to flowers of *Jatropha mutabilis* (Pohl) Baill. (Euphorbiaceae) in a Caatinga dry forest area, at the Catimbau National Park, Buíque, Pernambuco, Brazil

the self-fertilized progenies are less adapted to the environment than the cross-fertilized ones, geitonogamy will result in inbreeding depression (Husband and Schaemske 1996). Thus, the evolution of floral attractiveness depends directly on the trade-off between the benefits of attraction (higher number of visits, i.e., quantity of pollination) and the costs of geitonogamy (quality of pollination) (Williams 2007).

In conclusion, our findings show that plant-floral visitor interactions are sensitive to changes in the intraspecific number of open flowers/plot, independently of flower sex in monoecious species. In this sense, floral visitors can adjust the visitation rate according to resource distribution. Similarly, plant species can maximize floral visits by regulating flower production by opening fewer flowers per individual over a long period. The Caatinga dry forest, as a strongly seasonal environment, presents a limited availability of floral resources during the dry season. The continuous (i.e., all year round) and high production of flowers scattered among individuals, as in *Jatropha mutabilis*, increases the chances of pollination and allow the maintenance of plant species and floral visitors, which is especially important in seasonally dry tropical forests, such as the Caatinga dry forest.

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Author contributions JLSS and AVL conceived the study; JLSS collected the data; JLSS and OCN designed the experiments and analyzed the data; JLSS wrote the first draft of the manuscript; JLSS, OCN, and AVL wrote, revised and edited the manuscript.

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Declarations

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