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Do the traits of flowers and nectaries in *Sapium glandulosum* (Euphorbiaceae) shape insect interactions?

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Abstract
Ecological communities are shaped by intricate species interactions that influence ecosystem functions, stability, and biodiversity. Among these, plant-insect relationships play a particularly significant role in structuring ecological communities. The coevolution between plants and insects have been a key driver of their remarkable diversification, leading to a wide range of interactions, from mutualism to antagonism. In this study, we investigated the pollination biology of *Sapium glandulosum* (Euphorbiaceae) within a Cerrado palm swamp.We also recorded nectary visitors and identified the herbivores associated with the plant, particularly those specialized in feeding on latex. Our findings indicate that flies were the primary pollinators of *S. glandulosum*. Additionally, *Neolithus fasciatus* (Hemiptera) was the only herbivore observed; as its gall formation may allow it to bypass the plant's chemical defenses. Our results highlight the importance of Diptera as pollinators of *S. glandulosum* and the role of social wasps in regulating the herbivore population in the palm swamp.

Keywords Cerrado · Floral visitors · Insects · Social wasps · Nectary glands

Introduction

Ecological communities are shaped by a complex web of relationships among species populations that coexist over time and space (Webb et al. 2002). These interactions are crucial for maintaining ecosystem functions and support the stability and diversity of ecological communities (Huntly 1991; Barônio et al. 2016; Melo et al. 2018). Among these interactions, plant-insect relationships are particularly essential, as they significantly influence the composition and structure of ecological communities (Janzen 1970; Ollerton et al. 2011). The coevolutionary dynamics between plants and insects have been identified as a major driver of the remarkable diversification seen in these groups (Misof et al. 2014; Peters et al. 2017).

Plant-insect interactions are highly diverse, ranging from mutualistic relationships to those that can negatively affect at least one of the parties (Del-claro and Oliveira 1993; Sayers et al. 2019; Kobal et al. 2023). Among these, the mutualistic relationship of pollination between insects and flowering plants is especially well-studied and fundamental to the evolutionary success of both partners (Barônio et al. 2018; Torezan-Silingardi et al. 2021). Animal pollination is not only important for plant reproduction, but also contributes to the genetic variations of plant species (Murawski and Gilbert 1986; Bascompte and Jordano 2007). Insects, particularly bees, are key pollinators (Junqueira et al. 2021), though other insect groups, such as Coleoptera (beetles), Lepidoptera (butterfly and moths) and Diptera (flies), also play essential roles in plants of many families of Angiosperms (Rader et al. 2016; Saravy et al. 2021).

Just like pollinators, herbivores also exert strong pressure on plants. The evolutionary pressure exerted by both interactions is a compelling factor in the diversification of insects (Ehrlich and Raven 1964; Del-Claro and Torezan-silingardi 2021; LaFountain and Yuan 2023). Floral traits that attract

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pollinators can also be exploited by herbivores, who use these cues to locate host plants (Johnson et al. 2015; Stanton et al. 2016; Zilberman et al. 2023). In response to herbivory, plants have developed various defense mechanisms, including chemical deterrents, physical structures like trichomes and spines, and indirect defenses that attract natural enemies of herbivores, such as ants and spiders (Coley and Bryant 1985); Thornburg et al. 2003; Bezerra et al. 2021). For example, ants can reduce herbivore pressure while enhancing seed and fruit production (Del-claro and Marquis 2015). These plant defenses are often more effective when natural predators, such as ants and wasps, are present to remove herbivores (Marafeli et al. 2006; Torezan-silingardi 2011; Stefani et al. 2015). This illustrates how plants engage in intricate ecological networks to both mitigate herbivory and increase their chances of survival and reproduction (Gonzálvez et al. 2013).

Understanding the roles of various animal groups in plant-insect interactions is vital for advancing our knowledge of community ecology. This is particularly necessary in ecosystems where biodiversity is at risk, such as the Brazilian Savannah, also called Cerrado (Gottsberger 1994; Oliveira and Marquis 2002). Cerrado is the Brazilian second-largest biome, originally covering approximately 23% of the national territory. Cerrado presents many endemic species that may disappear as it is an endangered biome due to anthropogenic activities, as the expansion of cities, highways and farms, causing severe fragmentation of its area (Myers et al. 2000; Klink and Machado 2005 Gottsberger and Silberbauer-Gottsberger 2018) and both plant and animal populations are losing area nowadays. Cerrado contains a variety of vegetation types, including palm swamps, which feature both consistently moist and flooded central areas, and more variable peripheral zones (Araújo et al. 2002; Gottsberger and Silberbauer-Gottsberger 2018). Palm swamps are characterized by the presence of the palm tree *Mauritia flexuosa* (Arecaceae). These flooded areas play a crucial role in maintaining the geoecological equilibrium of the Cerrado (Araújo et al. 2002). The Euphorbiaceae family is widespread across Brazilian ecosystems, including in Cerrado palm swamps. *Sapium* (Euphorbiaceae) is a common genus within the Cerrado (Mantovani and Martins 1993; Batalha and Mantovani 2000; Tannus et al. 2006), and it consists of about 100 species of shrubs and trees producing latex, most of which are native to the Americas (Pscheidt 2011); Pscheidt and Cordeiro 2012).

Despite the prominence of *Sapium* in the Cerrado, little is known about their biotic interactions, including crucial information regarding the identity of pollinators for *Sapium* species, including the most common species in the genus, *S. glandulosum* (Pscheidt and Cordeiro 2012). However, the presence of specific foliar and floral structures may offer important clues about the nature of its ecological interactions. For instance, the reduced floral morphology—characterized by the corolla absence and no floral scent, pale yellow to green coloration, and openly exposed pollen and nectar (Pscheidt and Cordeiro 2012) —suggests a generalized pollination system. These traits facilitate unrestricted access to floral resources and are often associated with pollination by flies (Torezan-Silingardi 2021).

Sapium glandulosum also exhibits extrafloral nectaries (EFNs) located on the petiole. These glandular structures are not directly involved in pollination but are implicated in mutualistic interactions with generalist predators by secreting carbohydrate-rich nectar that attracts these organisms (Barbosa et al. 2025). In return, these predators may provide indirect defense against herbivores, a dynamic that supports the ecological function of EFNs under the protection hypothesis (Moura et al. 2023).

Complementing this indirect defense, *S. glandulosum* produces abundant latex, which acts as a potent physical and chemical barrier against herbivory (Fürstenberg-Hägg et al. 2013). The toxic compounds and the viscous nature of the latex exudate effectively restrict access by generalist herbivores, thereby favoring only those species specialized to overcome such defenses (Agrawal and Konno 2009).To address these gaps, our study explores the ecological relationships between *S. glandulosum* and its interacting arthropods. Specifically, we investigated its natural history within a Cerrado palm swamp and documented its ecological interactions. The central research questions driving this work are: 1.

Do the floral traits of *S. glandulosum* predict a generalist pollination system? 2) Are its extrafloral nectaries primarily involved in attracting predatory arthropods, while visitors of the nuptial nectaries act as pollinators? 3) Do its defensive traits (EFNs and latex) reduce herbivore diversity?

Materials and methods

Study area

The study was carried out in a preserved Cerrado area in the Savanna fragment of "Itororó Park Club" (Camargos and Lanna 1996), specifically in the palm swamp. The area is located at the geographical coordinates: 18° 60' S −48° 18' W (Araújo et al. 2002), south of the city center of Uberlândia, state of Minas Gerais, Brazil, with 640 hectares (Oliveira et al. 2009). The site has an elevation of 830 m above sea level (satellite data, Google Earth), an average annual rainfall of 1500 mm concentrated during the wet season (October – April), and an average annual temperature of 23 °C, with monthly temperature averages ranging from

24.8 °C in February to 19.9 °C in June (Alves-Silva and Del-Claro 2014). The palm swamp covers about 45 hectares and is well preserved, with a recorded 307 species distributed across 62 botanical families, with Poaceae, Asteraceae, Cyperaceae, Melastomataceae, and Fabaceae presenting the greatest species richness (Araújo et al. 2002).

Studied plant species

Sapium glandulosum (L.) Morong 1983 (Euphorbiaceae) is the species with the greatest occurrence within the genus. It is native to the Neotropical region and found from Argentina to Central America, particularly in areas with high humidity (Pscheidt and Cordeiro 2012). The specie produces large amount of latex, is heliophilous and deciduous, with a shrubby or arboreal growth habit, reaching heights between 5 and 20 m (Esser 1999). *Sapium glandulosum* is monoecious, with spike-shaped inflorescences on terminal branches, each inflorescence produces many unisexual flowers. Flowering and fruiting occur from September to April (Pscheidt and Cordeiro 2012). The leaves have a pair of conical-shaped extrafloral nectaries (EFNs) prominently displayed on the petiole (Santos and Sales 2009).

Floral biology and breeding system

Twenty floral buds were bagged in the pre-anthesis phase to avoid any damage during their development. They were distributed equally in four plants, five floral buds per plant. When the flowers opened, they were collected individually in plastic pots, taken to the Laboratory of Behavioral Ecology and Interactions in the Biology Institute of the Federal Univesrity of Uberlândia and observed under a stereomicroscope to characterize and quantify the carpels, locules, ovules, petals, and sepals. The quantity, viability, shape and coloration of pollen grains were investigated using 12 intact floral buds in pre-anthesis, collected in the morning, with two buds per plant from six individuals. The pollen grains were stained with acetic carmine, and 1000 grains were counted following the technique proposed by Kearns & Inouye (1993). The length of the inflorescence was measured with a caliper.

To investigate the breeding system floral buds were marked individually with cotton thread and enclosed in voile bags during the pre-anthesis phase to prevent contact with floral visitors. Five treatments were conducted, and fruit set was observed four weeks later. The following treatments were performed: (i) apomixis, in which 79 pistillate flower buds were isolated to prevent the arrival of pollen, (ii) spontaneous self-pollination, where 85 pistillate flowers from bisexual inflorescences were kept isolated to test the automatic transfer of pollen between staminate and pistillate flowers of the same inflorescence, (iii) manual self-pollination, where 85 pistillate flowers were manually pollinated with pollen produced by the anthers of the same plant, and (iv) manual cross-pollination, where 80 pistillate flowers were manually pollinated with pollen produced by the anthers of flowers from a different plant at least 20 m apart; (v) natural pollination or control group had 80 flowers that underwent open pollination, meaning they were freely accessible to insects in the area. A polyester tissue or Voal was used to prepare the bags used to isolate the floral buds and flowers.

Floral visitors

The observations of the fauna visiting the inflorescences were conducted on 25 individuals during a flowering period from December 2014 to April 2015. During this phase, 40 observations of 10 min were carried out, with at least two observations conducted each hour between 7:00 a.m. and 5:00 p.m. Each plant was observed at least once. The frequency and behavior of the visitors were recorded through focal observations. Images and videos were captured to document and analyze the behavior of the floral visitors. Specimens were collected using an entomological net and stored in individual vial. In the laboratory, all individuals were preserved in 70% ethanol. All collected insects were identified using key of species and subsequently classified into three functional groups, “Fly group”, “Wasp group” and “Other insects”.

Extrafloral nectary gland visitors

The fauna associated with the extrafloral glands present on the leaf petiole was observed on two observation periods, each one involved a total of 30 plants. The first period of observation occurred during the rainy months of the flowering season (from December 2014 to April 2015), and the second period took place during the dry season (from May to August 2018), a time when the plants do not produce inflorescences. All fauna foraging on the extrafloral nectary glands were recorded, collected, and taken to the laboratory for identification. The collection and preservation methods for the insects were the same as those used for the floral visitors.

Herbivores

In order to contribute to existing evidence suggesting that latex functions as a filter in plant–herbivore interactions, the abundance of herbivores associated with individual plants were quantified.All herbivores feeding on the flowers,

leaves, and sap were recorded. We also searched for cues left by chewing and piercing insects on the plant organs.

Based on the data collected, the structural complexity hypothesis proposed by Lawton (1978) was tested, which predicts that the architectural complexity of plants is positively correlated with herbivore species richness and abundance. For this hypothesis 12 adult plants were randomly selected to calculate the canopy volume. A measuring tape was used to measure the diameter, considering the branches furthest apart from each other, and the height of the tallest branch. For each individual plant, the number of galls on all aerial parts (leaves, inflorescences, stems and fruits) was counted.

Data analysies

The mean frequency of visitor species per flower, along with the standard deviation over time (measured every 10 min), was calculated since the initial anthesis process. For each observation, floral visitors were identified through focal observations on groups of four to five randomly selected inflorescences, with all visitors recorded. Additionally, the mean and standard deviation of visit frequency were calculated. Observations of all the animals feeding in the nectary glands during the dry period were analyzed using the Kruskal-Wallis test, and Spearman correlations were applied to examine relationships between arthropod abundances and environmental variables. To estimate canopy volume, the following formula was used $V = [4\pi\ (d+h/4)^3]/3$ where "d" represents canopy diameter and "h" the canopy height. To evaluate the relationship between plant volume and the abundance of the primary herbivore, Pearson's simple linear regression test was employed. All analyses, descriptive statistics, comparative data analyses and the visualizations were conducted using the R statistical environment (Core Team, 2024).

Results

Floral biology and breeding system

Sapium glandulosum exhibited terminal, spike-like inflorescences with unisexual flowers classified as racemes (Fig. 1). Two types of floral arrangement were found within the inflorescences. The first type was a unisexual inflorescence with only staminate or male flowers arranged in cymes. The second type was a bisexual or mixed inflorescence, with pistillate or female flowers in the basal/proximal portion and staminate flowers in the median and final/distal portion. Throughout flowering, very few mixed inflorescences were observed in which staminate flowers began to release pollen concurrently with the anthesis of pistillate flowers, however, the pistillate flowers of mixed inflorescences always initiated anthesis before the staminate flowers.

The inflorescences were exclusively located on the terminal branches of the plants, with female flowers positioned at the basal portion and male flowers at the distal portion of the inflorescence. The calyx consisted of small sepals that partially protect the ovary and the base of the filaments in the female and male flowers, respectively. There was no corolla in any flower. The pistillate flowers present green sepals, ovary, and style, while the stigma is yellow. The male flowers present orange-reddish anthers, green filaments, green-reddish sepals, and orange pollen grains. There was syncarpy in the pistil that was composed of three carpels fused at the ovary and style region, but the three stigmas were free. The ovary was superior, with three ovules, a single ovule in each of the three carpels, and the receptive stigma had a rough surface. The maturation of pistillate flowers always precedes that of the staminate flowers. Beneath male and female flowers there are two convex floral nectaries or nuptial nectaries of light green coloration. These nectaries become swollen and glossy during the floral anthesis of the adjacent flowers. No detectable odors, perceptible to the human sense of smell, were observed in either type of flower.

At the beginning of the reproductive period, when the young inflorescences measured between two and four centimeters, the small floral buds of both sexes displayed a green coloration. After the elongation phase of the inflorescences, it could achieve up to twelve centimeters, and if the female flowers were present, they were the first to bloom. The anthesis of the staminate flowers in bisexual inflorescences occurs after the senescence of the pistillate flowers or the onset of fruit development. During the pollen release phase, the flowers become more prominent in the environment, with a distinctive floral display due to the orange color of the pollen and the red of the anthers. At the end of the anthesis process, the anthers darken, and the stamens fall off. Then, the distal portion of the inflorescence begins to dry, and after a few days, a partial breakage of the raceme occurs leaving only the developing young fruits present. The physical changes experienced by the pistillate flower, from the bud phase to post-pollination, are presented in Fig. 2. The mature fruit was dark greenish-brown and consisted of a rounded capsule divided into three segments, each capable of developing a single seed covered by a red aril.

The beginning of flowering was not simultaneous among individuals, with only 41.93% of plants already in flower in the first week of October 2019. Weekly observations throughout the flowering period showed that most individuals did not flower. The plants that flowered presented inflorescences of both types. Initially, plants with mixed



Fig. 1 (**a**) The bisexual or mixed inflorescence, with pistillate or female flowers in the proximal portion and staminate flowers in the distal portion. (**b**) Unisexual inflorescence with only staminate flowers arranged in cymes

inflorescences and, plants with only male inflorescences were found. Plants with only male inflorescences decreased their flower production after the middle of the first month of flowering onset. The mixed inflorescences were produced throughout flowering, but in smaller quantities at the beginning. Each pistillate flower had about 2,691 pollen grains, with high pollen viability (89.5%) (Fig. 3).

Pollination tests demonstrated that the reproductive system accepts a very low rate of self-reproduction (Table 1), however, it was not possible to test whether female and male flowers from the same inflorescence could self-pollinate since the maturation of them does not occur simultaneously (Table 2).

Floral visitors

Insects from the orders Hymenoptera, Diptera, Coleoptera, Blattodea, Hemiptera, and Lepidoptera were observed visiting the inflorescences of *S. glandulosum* (Table 2). We categorized these visitors into three groups: the "Diptera Group," comprising insects from the families Calliphoridae, Sarcophagidae, and Syrphidae; the "Hymenoptera Group," including many social wasps as Cabronidae and Pompilidae, and Apidae with some small bees; and the "Other Insects" group, which included the remaining orders Coleoptera, Blattodea, Hemiptera, and Lepidoptera. Among these six orders, Diptera and Hymenoptera represented 93% of all visits to the inflorescences (Fig. 4). Flies were the most frequent visitors, with 176 recorded visits, followed by Hymenoptera species with 116 visits, and the Other Insects group with 26 visits. The least frequent visitors included single observations of Blattodea, Meliponini (Apidae), and *Pepsis* (Pompilidae).

Flies foraged on the inflorescences primarily in search of nectar from the nuptial glands just below the flowers, both female and male flowers. As they moved over the inflorescences, the flies inadvertently collected pollen on the hairs from the ventral parts of their bodies (Fig. 5). This pollen

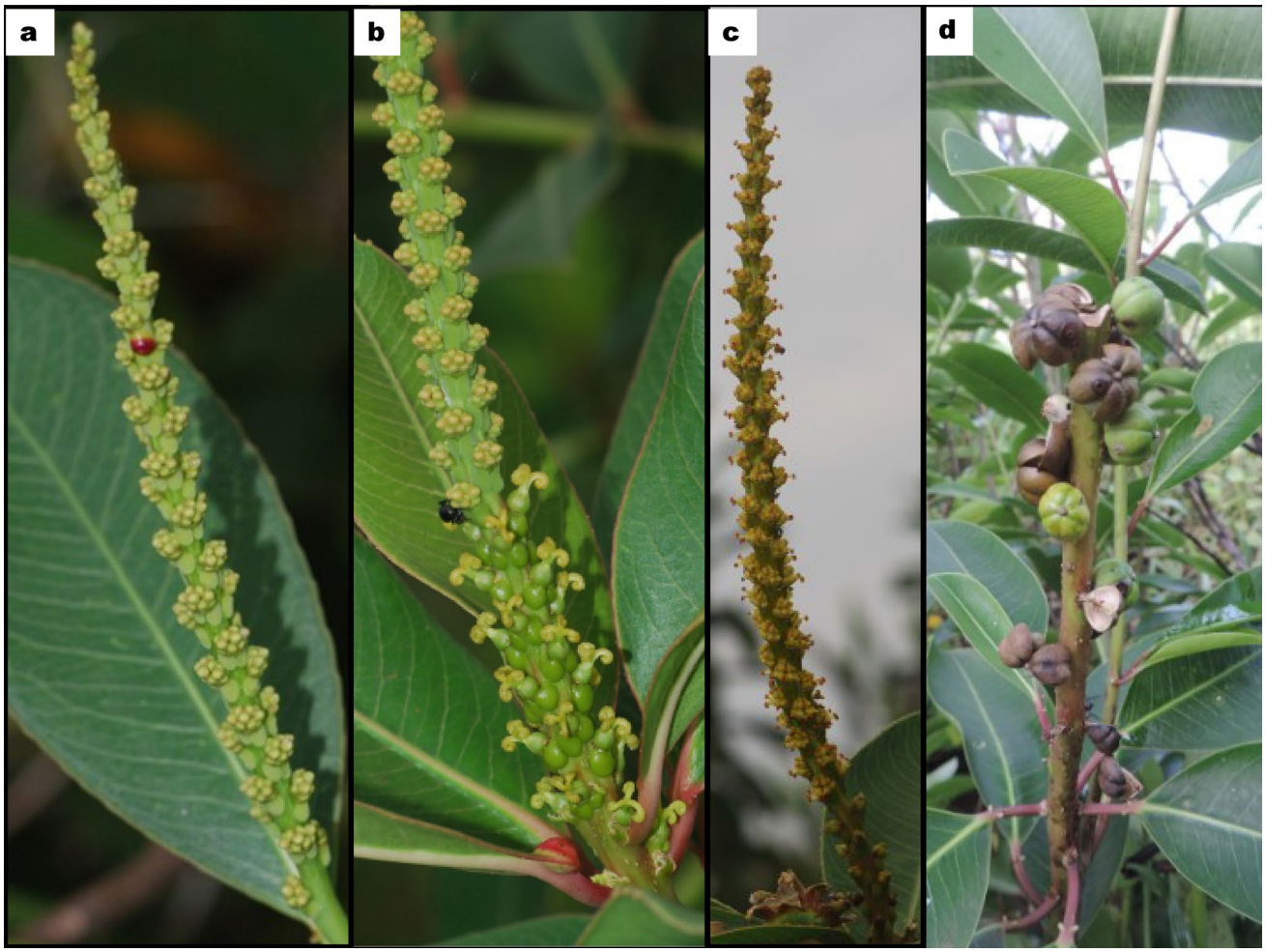


Fig. 2 Floral phases of the inflorescences of *Sapium glandulosum*. (**a**) Inflorescence with floral buds (note the red-colored gall). (**b**) Inflorescence with receptive female flowers at the lower portion of the cymes and male floral buds at the upper portion. (**c**) Male flowers with pollen available to floral visitors at the upper portion; senescent female flowers at the base. (**d**) Natural abscission of the upper part of the cymes, leaving only fruits located at the lower portion

was subsequently deposited onto the receptive stigmas as the flies passed over the female flowers, facilitating pollination. Flies were observed every day of observation, and no active pollen collection was noted.

Extrafloral nectary gland visitors

During the first observation period, when flowers were produced, the most frequent group was Hymenoptera with 161 visits, followed by Diptera with 110 visits, all other insects were responsible for only 34 visits (Fig. 6). The most frequent visitors of extrafloral nectaries were the social wasps 134 visits (44%) (Fig. 7).

In the second period of observation, during the vegetative phase in the dry period, arthropod visitation was low in the early hours of the day, with a gradual increase that followed the rise in temperature until the hottest hours of the day, and then there was a gradual decrease that followed the decrease in temperature until twilight (Fig. 8). There was a significant difference in insect abundance on *S. glandulosum* during the daytime, with a significant predominance during the hottest hours of the day, between 11 am and 3 pm (Kruskal-Wallis chi-squared = 21.3, df = 9, $p = 0.01138$).

Herbivory

No exophytic animal was recorded cutting, sucking, or chewing the leaves. However, one species of endophytic insect was very common among the 46 plants observed, the gall-inducer *Neolithus fasciatus* Scott, 1882 (Hemiptera: Triozidae) (Fig. 9). During the peak of the flowering period (January 2015), plants exhibited a wide variation in the number of galls (ranging from just one to 260), within which the insect developed from egg to adult stage. When the inflorescences of *S. glandulosum* present lots of *N. fasciatus* galls, fruits are aborted (Fig. 10). The Pearson statistical test

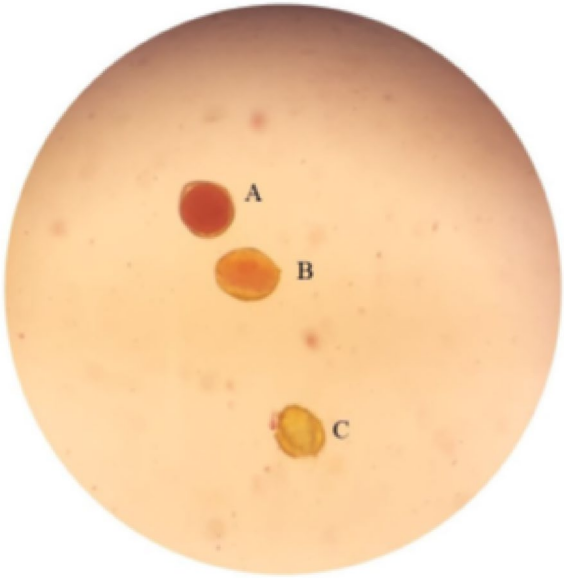


Fig. 3 Pollen grains of *S. glandulosum* after Carmin acetic treatment in microscopic view. (**A**) Indicating viable, and non-viable (**B** and **C**) pollen grains

Table 1 Breeding system of *S. glandulosum*, considering the quantity of female flowers used in each treatment, fruits produced, fruit set, and the number of seeds of each pollination treatment

Treatment	Flowers/fruits	Fruit set (%)	Total seeds
Agamospermy	79/0	0	0
Spontaneous Self-pollination	85/1	1.1	3
Manual Self-pollination	40/1	2.5	3
Cross-pollination	80/17	21.2	51
Natural pollination	80/31	38.7	93

indicated a positive relationship between the volume of the canopy and the number of galls, with an adjusted R^2 value of 0.627 ($F_{1, 11} = 19.529$; $p = 0.001$) (Fig. 11). Occasionally, we observed the social wasp *Polybia scutellaris* capturing the adults *N. fasciatus* gall-inducers on the plants. This wasp showed the highest abundance in the foliar nectaries (EFNs) (21.8%).

The social wasp species *Polybia scutellaris* White, 1841 and *Synoeca cyanea* Fabricius, 1775 (Vespidae) were observed capturing both adult and immature *N. fasciatus* individuals. *Synoeca cyanea* was also observed opening and removing an immature *N. fasciatus* from within a gall on *S. glandulosum*.

Discussion

Sapium glandulosum showed to be self-incompatible, relying on pollinators for fruit and seed production. Our observations indicated that the primary pollinators are insects,

Table 2 Insect visitors of *S. glandulosum* and resources they collected from the plant during the flowering season

Visitors	Resources Consumed
Diptera	
Calliphoridae	
*Chrysomya**	Nuptial and extra floral nectar
*Lucilia**	Nuptial and extra floral nectar
Sarcophagidae	
*Sarcodexia**	Nuptial and extra floral nectar
Syrphidae	
Shirphini	Nuptial and extra floral nectar
Hymenoptera	
Apidae	
Meliponini	Pollen
Cabronidae	Pollen and nuptial nectar
Formicidae	Extra floral nectar
Pompilidae	
Pepsis	Nuptial nectar
Vespidae	
Polybia	Nuptial and extra floral nectar
Agelaia	Nuptial and extra floral nectar
Polistes	Nuptial and extra floral nectar
Synoeca	Nuptial and extra floral nectar
Coleoptera	Nuptial and extra floral nectar
Blattodea	Nuptial and extra floral nectar
Hemiptera	Nuptial nectar
Lepidoptera	Nuptial nectar

The plant provides nuptial nectar from glands located in the inflorescence and extrafloral nectar from glands located in the foliar petiole. *Potentials pollinators

particularly Diptera species from the families Calliphoridae, Sarcophagidae, and Syrphidae. Flies are attracted to the nuptial nectaries near the flowers and the extrafloral nectaries present in the petiole of the leaves. In addition to nectar intake, pollen can also be consumed as food. Furthermore, it is likely that the EFNs function as an indirect defense mechanism for the plant by attracting Vespidae species. The main visitors to the EFNs were social wasps, which foraged on the nectaries and were observed preying on the primary herbivore of *S. glandulosum*, the gall-inducing *N. fasciatus.* This was the only herbivore species recorded on *S. glandulosum.* The low diversity of herbivorous insects may be explained by the presence of latex in *S. glandulosum*, and the presence of many young plants in the area may explain why some plants did not bloom during the observation period.

The floral biology considered many aspects, including the type of inflorescence produced by *S. glandulosum.* The inflorescence structure observed in this study closely resembles that found in other Euphorbiaceae species, particularly monoecious species with unisexual flowers. These flowers are produced in inflorescences containing only staminate flowers or in bisexual ones, those with both staminate and pistillate flowers (Medeiros Silva et al. 2006; Neves et al. 2011). The protogyny observed in the bisexual

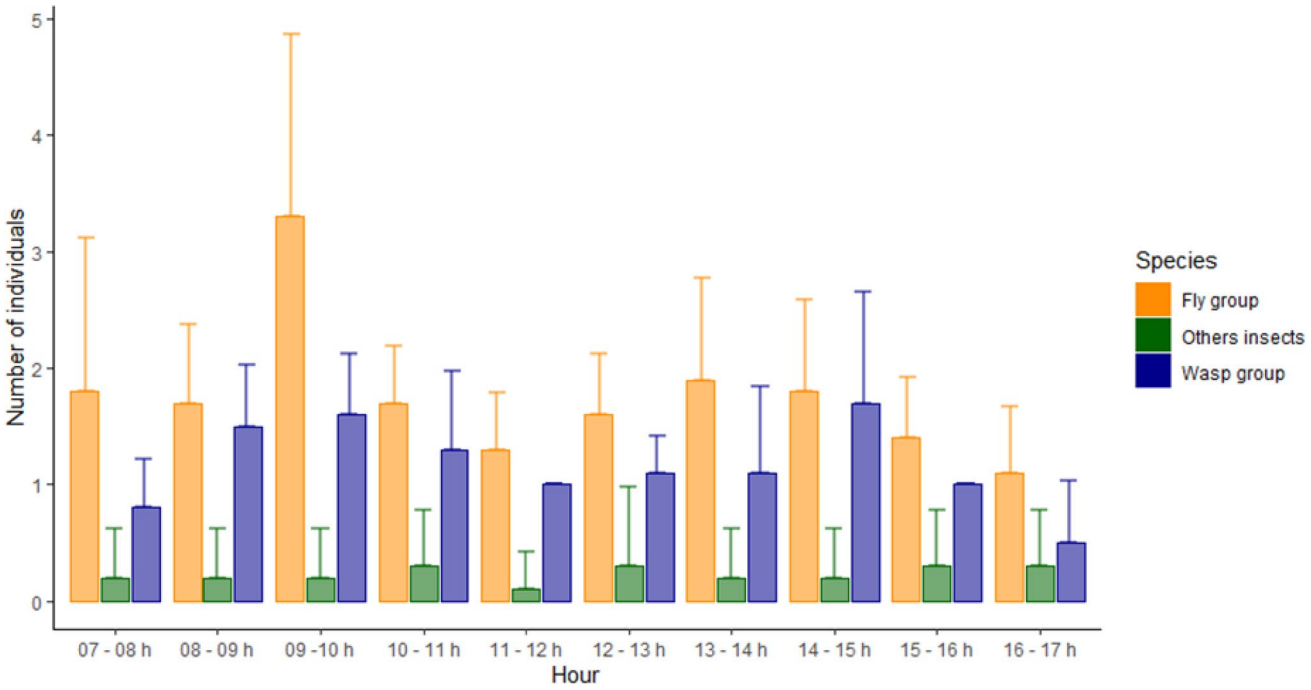


Fig. 4 Number (mean ± SD) of visitors per inflorescence of *S. glandulosum* from 7–17 h

inflorescences here is a mechanism where pistillate flowers bloom before staminate flowers, this process reduces self-pollination, consequently increasing cross-pollination success but it is rare in nature (Lloyd and Webb 1986)Functional dioecy, another mechanism favoring cross-pollination, was observed in 46% of *S. glandulosum* individuals during the initial blooming period, when those plants produced inflorescences exclusively with staminate flowers, rendering them functionally male.

In monoecious species, the number of staminate flowers often exceeds that of pistillate flowers due to the lower energetic cost of producing the pollen grains in the staminate flower, compared to the higher cost of developing the seed and fruit in pistillate flower (Araújo et al. 2002)). This reproductive strategy was reflected in the findings of this study: even after the third week of flowering, when fewer plants produced exclusively staminate inflorescences, the number of staminate flowers remained significantly higher than that of pistillate flowers, consistent with results reported by Cardoso (2016).

The floral biology of *S. glandulosum* documented in this study also aligns with descriptions from two other researches on the same species (Sátiro and Roque 2008; Santos and Sales 2009). However, while Santos and Sales (2009) and Santos et al. (2018) recorded 2–3 carpels and locules, this study consistently found 3 carpels and 3 locules, each containing a single ovule, in agreement with findings by Hiura (2011) and Cardoso (2016). *Sapium glandulosum* is recognized as the species with the highest degree of morphological or phenotypic plasticity within its genus indicating that the variations noted by different researchers may reflect its inherent polymorphism (Esser 1999). The presence of many young plants in the area may explain why some plants did not bloom during the observations.

Although floral syndromes may predict a pollinator different from what is observed in the field (Kobal et al. 2024) the floral traits of *S. glandulosum* exhibit characteristics entomophily. The observations made on *S. glandulosum* flowers highlights that the primary pollinators are members of the order Diptera. Among the flower visitors, fly species showed the highest visitation rates, demonstrating suitable behavior, frequency, and morphology for effective pollination. Although often overlooked, flies represent the second largest group of flower pollinators and visitors worldwide, with 79 out of 159 recognized families relying on flowers for feed on pollen and nectar (Wardhaugh 2015). Diptera-mediated pollination is documented in over 500 plant species and more than 100 cultivated crops, including mango, cocoa, and apple (Inouye et al. 2015; Wardhaugh 2015; Rader et al. 2016; Wolowski et al. 2019). Additionally,, some Diptera species engage in deceptive pollination strategies, in which plants attract spollinators without providing a reward (Gaskett 2011; van der Niet et al. 2011; Inouye et al. 2015). Numerous flies were observed in the inflorescences of *S. glandulosum*, with substantial quantities of pollen attached to the head, legs, and ventral side of their bodies. Pollen transfer to stigmas was noted when these



Fig. 5 Diptera collecting resources from *S. glandulosum* in the wetland of the ecological reserve at Clube de Caça e Pesca Itororó de Uberlândia. (**a**) and (**b**) Diptera searching for nectar in glands. (**c**) and (**d**) Diptera feeding on secretions from glands associated with the staminate flowers on the rachis of the inflorescence. Note that in all individuals, many pollen grains adhere to the hairs on the legs, abdomen, and even the heads of the flies

pollen-bearing flies foraged on the nuptial nectaries near the pistillate flowers.

Myophily, or pollination by flies, is uncommon in the Cerrado biome, where bees are typically the dominant pollinators (Gottsberger and Silberbauer-Gottsberger 2018). During the observation period, however, only a single bee (Meliponini) was recorded visiting the flowers. This may be attributed to the morphology of *S. glandulosum* inflorescences, which are characterized by small, scentless flowers that lack corollas, provide easy access to pollen, and have nectar glands (Santos and Sales 2009; Pscheidt and Cordeiro 2012). These floral traits align more closely with myophily (Torezan-Silingardi et al 2021), featuring understated pistillate flowers in shades of yellow and green, while the staminate flowers are more conspicuous with orange-red anthers attached to green calyces. Flies from the family *Calliphoridae*, for example, are known to favor red colors (Gong et al. 2015), which may explain their frequent visitation to these inflorescences.

Tritrophic interactions linked *S. glandulosum*, its herbivores and their predators. The diversity of herbivores and degree of damage were reduced due to the plant's protection offered by the latex production and by the wasps attracted by the NEFs, acting as an effective defense against herbivory (Barônio 2012; Stefani et al. 2015; Rosa et al. 2024). Only a limited group of insects, such as the gall-making *N. fasciatus*, which has evolved the ability to avoid or tolerate the latex's toxicity, can feed on *S. glandulosum* tissues.

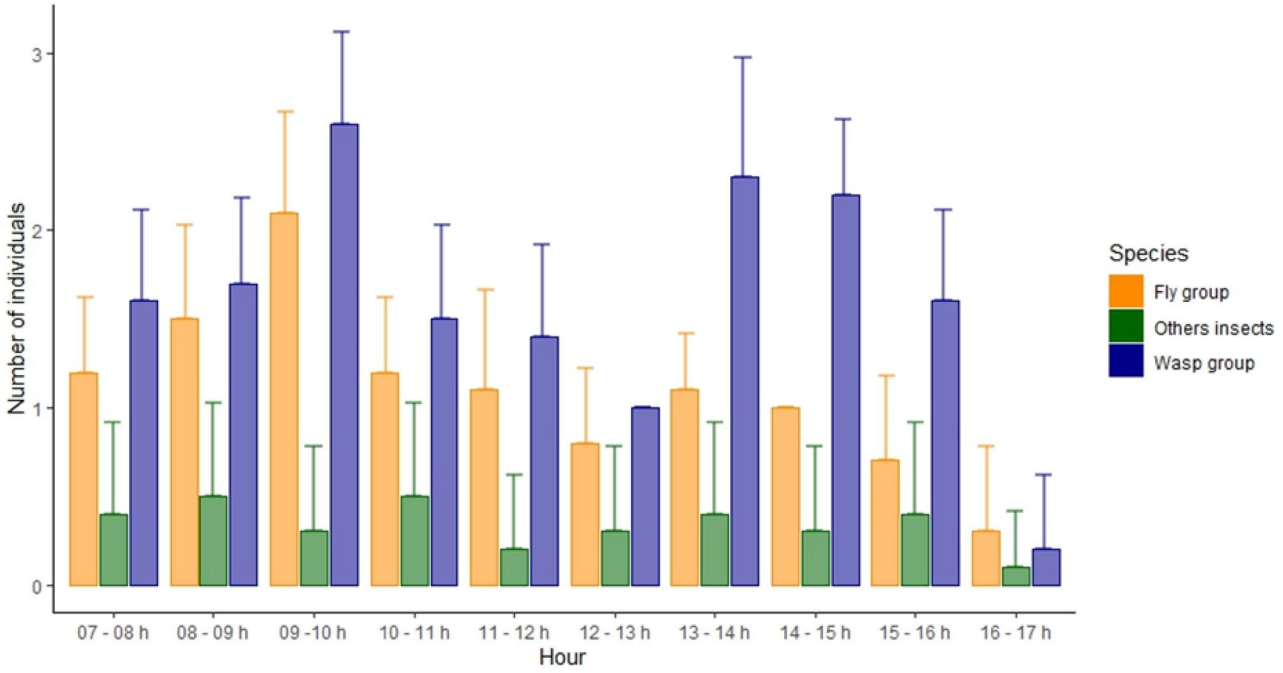


Fig. 6 Number (mean ± SD) of visitors per extra floral nectaries of *S. glandulosum* from 7–17 h

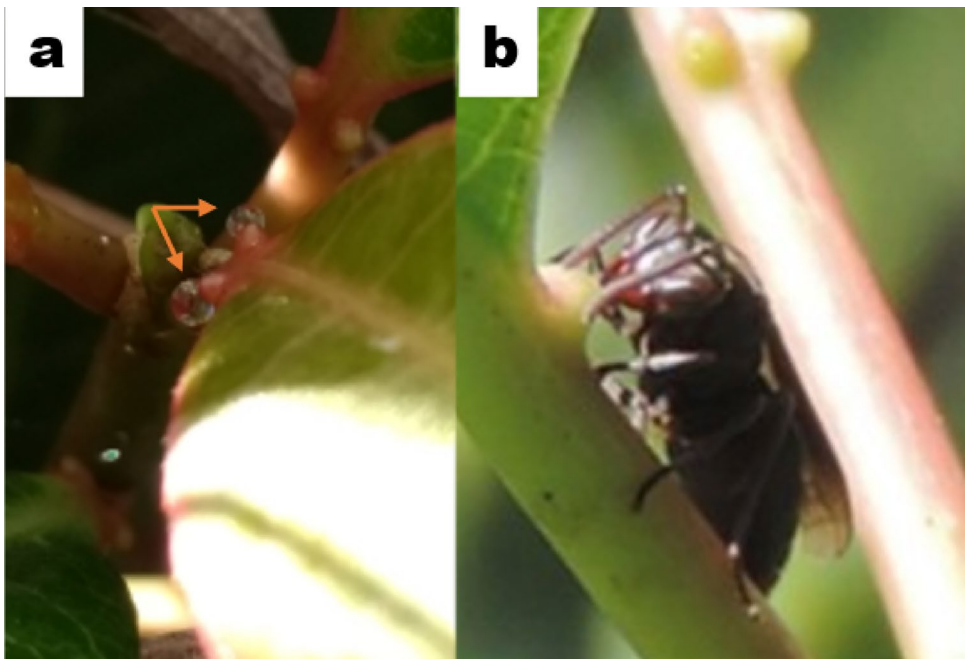


Fig. 7 Extrafloral nectary glands. (**a**) Extrafloral glands producing nectar (orange arrows) (**b**) *Polybia scutellaris* (Hymenoptera: Vespidae) feeding on the extrafloral nectaries of the leaf petiole

N. fasciatus was also observed on another host plant of the same genus, *S. aucuparium* (Fernandes et al. 2014). Higher infestations of *N. fasciatus* are associated with larger plants, likely due to the greater availability of resources. This pattern aligns with other studies that have linked increased herbivory to larger, mature plants with more abundant foliage (Lawton 1983; Loyola and Fernandes 1993; Araújo and Santos 2009). These findings, along with those of the present study, support the structural complexity hypothesis (Lawton 1983), which proposes that structural complexity in plants correlates with greater richness and abundance of herbivorous species.

The Euphorbiaceae family is among the richest gall-making species within dry forests (Fernandes et al. 2014)). Galls protect the developing immature herbivore inside the plants tissue, avoiding many predators to find these developing gall-makers. But as observed here, some wasp species can open the gall and prey on them. Additionally, to the

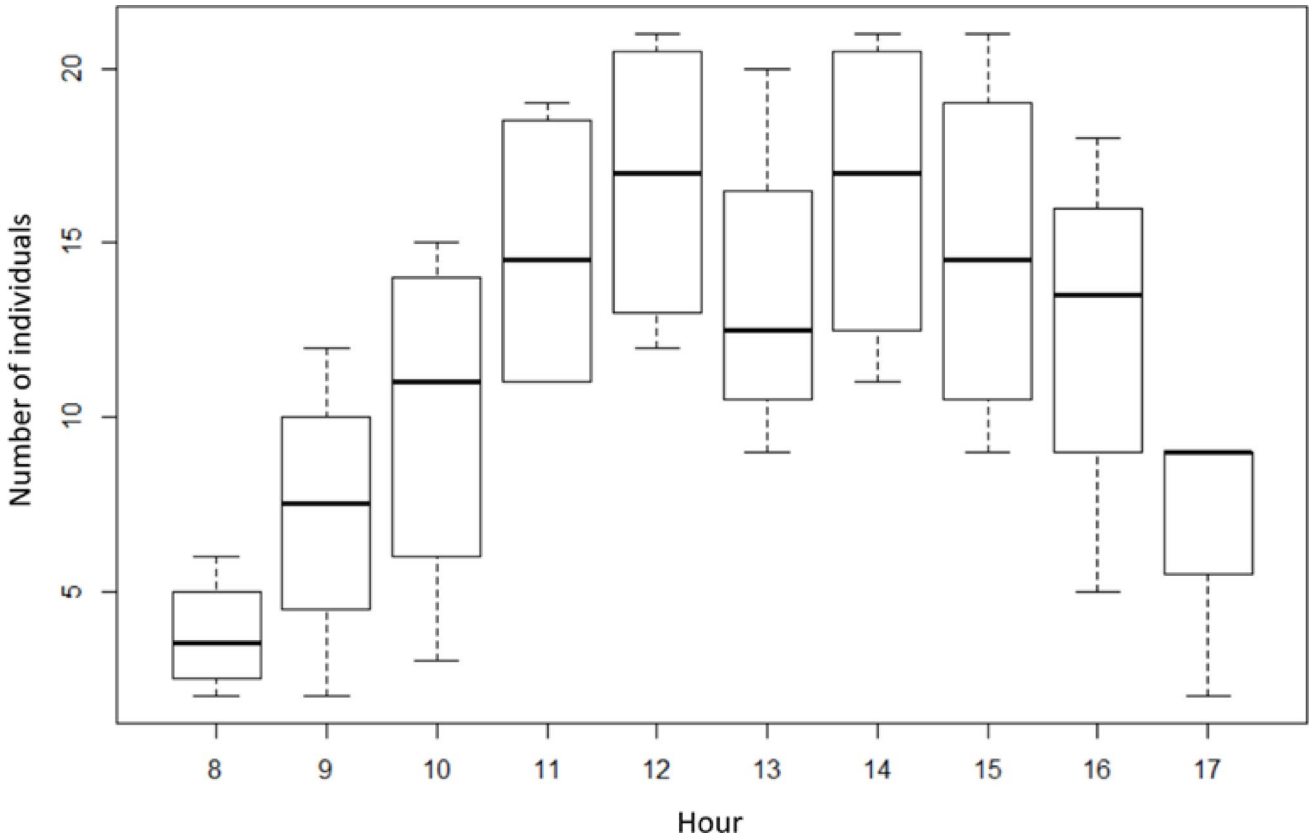


Fig. 8 Diurnal variation in arthropod abundance on *Sapium glandulosum*

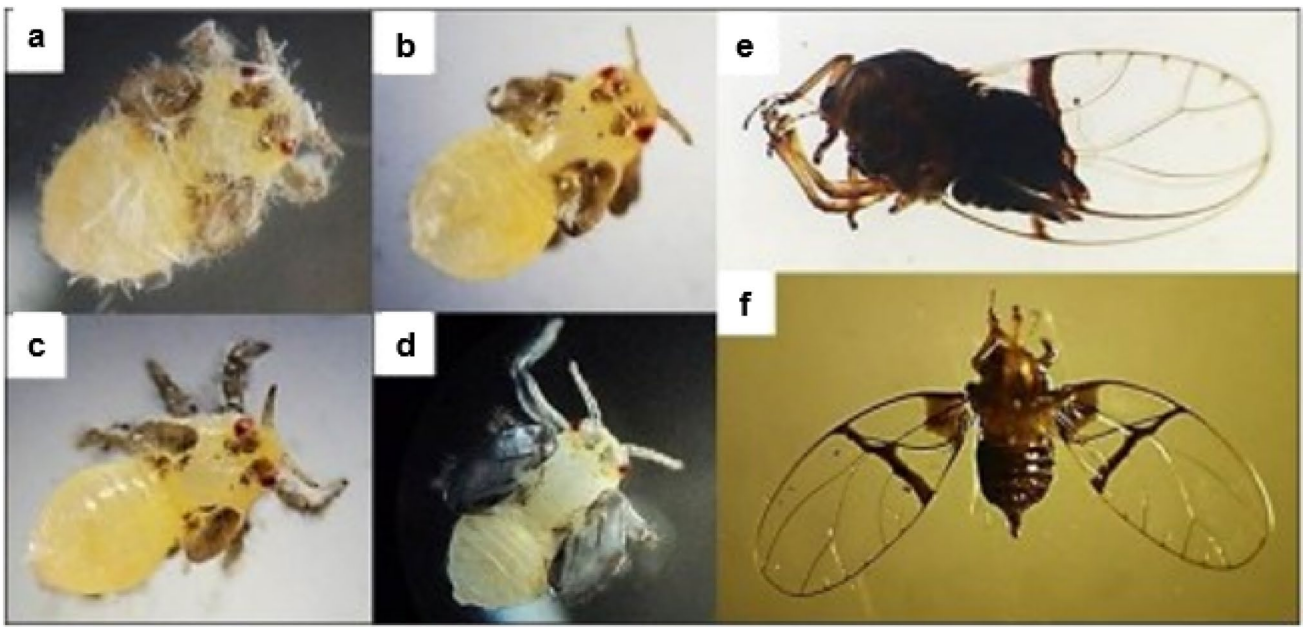


Fig. 9 *Neolithus fasciatus* gall-inducing insect in different developmental stages during the flowering season of *S. glandulosum*. The nymph develops inside the gall (**a** to **d**), while the adult insect (**e**, **f**) is free-living



Fig. 10 Galls in inflorescence of *Sapium glandulosum* and after the emergence of the *N. fasciatus* adults

latex protection, plants provide highly nutritious resources through the extrafloral nectaries that can attract ants (Lange et al. 2017), spiders (Dias and Stefani 2024), and wasps (Brock et al. 2021), which prey intensely on herbivorous.

This study is the first to document *P. scutellaris* (Vespidae) capturing adult of *N. fasciatus* and *S. cyanea* (Vespidae) capturing its larvae. There are records of solitary and social wasps in the same savannah area capturing endophytic beetle larvae when the wasps use their mandibles to break through plant tissues (Torezan-silingardi 2011; Alves-Silva et al. 2013). Similarly, *S. cyanea* exhibits the same behavior by extracting the immature stages of *N. fasciatus* from within the galls. Social wasps play a crucial role in controlling herbivore populations by preying on these insects. The ecological interaction between social wasps and *S. glandulosum* observed in this study may be characterized as mutualistic: the wasps reduce herbivory pressure on *S. glandulosum* by removing its primary gall-maker, while the wasps benefit by foraging at those larvae and at the EFNs. However, further research is needed to test these hypotheses. For example, experiments involving wasp exclusion, measurements of fruit set, or assessments of herbivore damage in individuals with varying levels of wasp visitation could provide valuable insights into the defensive role of social wasps in *S. glandulosum*. These EFNs provide a reliable nectar source and act as ambush points for capturing other arthropods attracted to the plant. In 2023, for the first time, *Polybia fastidiosuscula* Saussure, 1854, *P. scutellaris* (White, 1841), and *Protopolybia sedula* (Saussure, 1854) were recorded feeding on EFNs of another plant from the same genera studied here, *S. obovatum* (Oliveira et al. 2023). Although social wasp foraging at EFNs is not so common, it appears to be a generalist behavior (Alves-Silva et al. 2013; Oliveira et al. 2023). Limited research exists on the ecological relationships between wasps and EFNs.

Neolithus fasciathus can reduce the fitness of *S. glandulosum* when galls are formed on its inflorescences. Our observations reveal that an inflorescence filled of galls has its development disrupted, resulting in complete fruit

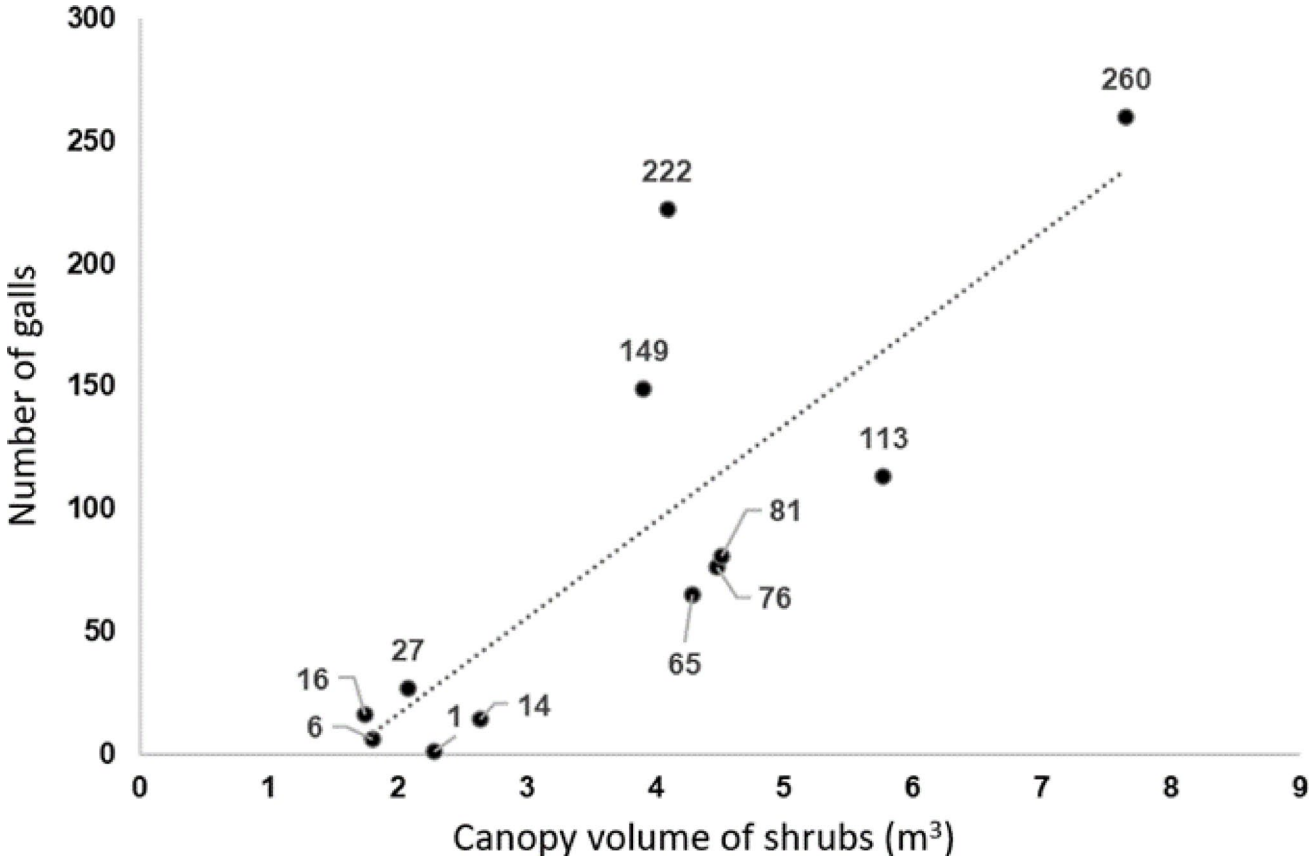


Fig. 11 Number of galls related to the canopy volume of *S. glandulosum*

abortion. Therefore, social wasps may indirectly benefit the fitness of *S. glandulosum*.

The frequent presence of social wasps at extrafloral nectaries can be better understood by considering their lifestyle. Vespidae are primarily predatory, adults consume nectar and pollen, while the immature wasps receive animal protein from prey captured by adults (Torezan-silingardi 2011; Alves-Silva et al. 2013). Further research is needed to determine whether wasps are attracted by specific chemical signals released by the plant, as the release of organic volatiles to recruit predators is well-known in ecological studies.

Conclusion

This research represents the first contribution to the field of pollination studies for the genus *Sapium*. Despite encompassing over 100 species, no prior research has investigated the pollination mechanisms within this genus. Ecological studies on *Sapium* are notably scarce, as most existing research has focused on species surveys, morphological descriptions, and pharmacological properties, primarily due to the genus's production of latex. The findings of this study reveal that *S. glandulosum* is self-incompatible, with some individuals displaying functional dioecy (Fig. 11).

All three hypotheses proposed in this study were supported by the observed data and existing literature. First, our results align with previous studies showing that flowers with easily accessible floral resources—such as exposed pollen and nectar—are typically visited and pollinated by generalist insects, particularly flies and bees. Second, the role of extrafloral nectaries (EFNs) in attracting predatory arthropods was confirmed. EFNs were primarily visited by predators, which were observed actively preying upon the plant's main herbivore, thereby supporting their function as an indirect defense mechanism. Most fly individuals visited the nuptial nectaries, and their behavior identified them as the pollen vectors. Finally, the third hypothesis was also validated. According to the literature, latex functions as a strong herbivore filter, limiting access to foliar tissues and allowing only specialized herbivores to feed on the plant. Collectively, these findings reinforce the ecological relevance of floral traits, EFNs, and latex in mediating the biotic interactions of *S. glandulosum*.

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Author contributions ROACK and HMTS originally formulated the idea, and conceptualization, ROACK, RSA and ARF conducted fieldwork, investigation and performed statistical analyses, ROACK, RSA, ARF and HMTS writing – review and editing, ROACK wrote the original draft.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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