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Abundance vs. Efficiency: The role of *Apis mellifera* and *Trigona spinipes* in the Pollination of the Star Fruit Tree (*Averrhoa carambola* L.)

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Abstract

The star fruit tree (*Averrhoa carambola* L.) has knowledge gaps regarding its reproductive dynamics and interactions with pollinators under field conditions. This study aimed to characterize the phenology, floral biology, and efficiency of biotic visitors in fruit set in Brazil. Flowering occurred from December to February (~90 days), with synchrony among individuals. The flowers are hermaphroditic, ephemeral (with a longevity of 12 h), and exhibit morning anthesis (07:00), with stigmatic receptivity maintained throughout the floral opening period. Floral density was high, with an average of 21.22 ± 11.36 flowers per inflorescence. The visiting entomofauna was predominantly Hymenoptera (95.3%), with *Trigona spinipes* (58.3%) and *Apis mellifera* (37%) the most prominent. However, resource segregation was observed: *T. spinipes* acted primarily as a resin collector, while *A. mellifera* collected nectar exclusively, exhibiting a significantly higher foraging rate (10.15 ± 1.28 flowers/min) compared to *T. spinipes* (4.69 ± 1.40 flowers/min). In pollination tests, there was a significant difference ($p < 0.05$) between all treatments: pollination directed by *A. mellifera* resulted in the highest initial fruit set (3.1%), followed by free pollination (1.9%) and wind/phyllo pollination (1.2%). Total isolation (paper bags) produced only 0.5% of fruits, confirming that spontaneous self-pollination is inefficient due to floral morphology. It is concluded that, despite the abundance of *T. spinipes*, it does not effectively contribute to pollination because it focuses on non-reproductive resources. A. *mellifera* is the most efficient pollinator. Its targeted introduction is essential to mitigate pollination deficits and increase star fruit productivity.

Introduction

Approximately 87% of the world's wild flowering plants are pollinated by insects and other animals (Zattara & Aizen, 2021); more than three-quarters of the world's major food crops benefit, at least partially, from biotic pollination; and it is estimated that one-third of the global food supply is directly benefited by biotic pollination (Potts et al., 2017; Ellis et al., 2020). The economic value of this biological interaction is colossal: global estimates indicate that pollination services contribute between US$ 235 billion and US$ 577 billion annually (IPBES, 2016). In Brazil, a country with a predominantly agricultural vocation, the value of this ecological service is estimated at around US$12 billion per year, supporting crops of high economic and strategic value, such as coffee (*Coffea arabica* L.), oranges (*Citrus sinensis* L. Osbeck), and soybeans (*Glycine max* L. Merr.). Dicks et al. (2021) highlight that food security depends directly on the conservation of pollinators, as approximately 75% of food crops worldwide require, to some extent, biotic pollination, with this dependence being particularly relevant for fruit crops.

Despite its unquestionable importance, the pollination service faces an unprecedented crisis, often referred to as the "global pollination crisis." The contemporary model of

agricultural expansion, characterized by the extensive increase in cultivated areas to meet the growing demands of the consumer market, has generated severe negative externalities. The intensive and often inappropriate use of land, coupled with systematic deforestation, fires, and habitat fragmentation, has accelerated the degradation of natural ecosystems (Gazzoni et al., 2025). Such anthropogenic alterations result in the loss of nesting refuges and a drastic reduction in foraging sources for pollinators (Razo-León et al., 2025; Aguilar et al., 2025).

Additionally, the widespread use of pesticides poses a direct threat to the integrity of pollinator populations. New-generation insecticides, such as neonicotinoids, contain neurotoxic components that, even at sublethal doses, compromise bees' ability to orient, learn, and collect resources (Ahsan et al., 2025). This scenario is exacerbated by global climate change, which alters plant phenological cycles and species' geographical distributions, potentially leading to a "temporal mismatch" between flowering and pollinator emergence, thereby disrupting historical co-evolutionary interactions (Oliveira et al., 2025; Peng et al., 2025). Consequently, wild pollinators are no longer sufficient to guarantee adequate pollination of various crops in several regions of the world (Gallai et al., 2009).

To mitigate these impacts and avoid the costly production due to low productivity, the managed introduction of pollinators in agricultural areas has become an indispensable practice (Sáez et al., 2022). The social bee *Apis mellifera* L. is the most widely used species worldwide in directed pollination programs due to its ease of management, large colony size, and generalist behavior (polylegia). The presence of *A. mellifera* in crops not only maximizes the fruit set rate but also substantially improves the qualitative parameters of the fruits, such as mass, shape, size, and shelf life (Free, 1993).

In Brazil, however, the systematic use of managed pollinators is still incipient and concentrated in a few economically significant crops, such as apples (*Malus domestica*) in the South and melons (*Cucumis melo*) in the Northeast (IBGE, 2025). In much of the country, the misconception prevails among producers and beekeepers that the mere presence of a few colonies near the planting area is sufficient to guarantee ideal pollination rates. This technical negligence results in under-pollinated crops, leading to low profitability and contributing to the devaluation of environmental services in the national agribusiness sector (Milfont et al., 2013). This scenario is primarily due to a lack of technical knowledge about floral characteristics, insect behavior, and the specific pollination needs of many tropical crops.

Among the fruit trees with expansion potential that lack in-depth studies, the star fruit tree (*Averrhoa carambola* L., Oxalidaceae) stands out. Originating in Asia, the star fruit is widely cultivated in tropical and subtropical regions, with significant production in Malaysia, Taiwan, and Brazil. In the Brazilian market, the crop generates significant revenue and is an important source of income for small and medium-sized producers (Bastos, 2004). However, despite its commercial value and export potential to demanding markets such as Europe and the United States (Donadio et al., 2001), management techniques for star fruit pollination remain uncommon in Brazil.

The reproductive biology of *A. carambola* is complex. The species exhibits varying degrees of self-incompatibility and is often considered self-sterile (Knight, 1965). As sessile organisms, these plants depend entirely on biotic agents that mediate the transport of pollen between genetically distinct individuals (cross-pollination) for fertilization and the formation of viable fruits and seeds (Gao, 2025). Without efficient pollinators, the star fruit tree exhibits extensive floral abortion and low fruit production.

Classic studies conducted in Malaysia indicate that the honeybee *Trigona thoracica* is among the most efficient wild pollinators of this crop (Phoon et al., 1984). However, this species is endemic to Asia and does not occur in the Americas (Rasmussen, 2008), necessitating the identification of local pollinators or the use of cosmopolitan species to fulfill this role in Brazil. Although the star fruit tree is considered highly dependent on bees (Giannini et al., 2015b), especially *Apis mellifera* (Ray, 2002), the exact degree of this crop's dependence on pollinators under Brazilian climatic conditions remains an academic enigma (Giannini et al., 2015a). The available literature is scarce and mostly composed of studies conducted in North America and Asia many decades ago (Knight, 1965, 1982; Phoon, 1984).

Considering the need to enable the expansion of star fruit cultivation and optimize its yield without increasing the cultivated area, which is in line with the principles of sustainable agricultural intensification, it is imperative to develop research that elucidates its interaction with pollinators. Understanding the pollinating efficiency of *A. mellifera* in star fruit can support the development of colony management protocols, allowing producers to use pollination services as a strategic agricultural input to improve orchard quality and productivity.

Given this scenario, the present study aimed to characterize the reproductive phenology and floral biology of *Averrhoa carambola* L., identify the visiting entomofauna, and analyze the foraging behavior of the predominant species. Additionally, it sought to evaluate the efficiency of different pollination methods in the initial fruit set, aiming to determine the role of biotic vectors and the existence of pollination deficits.

Materials and Methods

Location and Characterization of the Study Area

The experiment was installed in a star fruit (*Averrhoa carambola* L.) orchard belonging to the Experimental Station of the IPA - Agronomic Institute of Pernambuco, located in the municipality of Brejão, in the Agreste region of Pernambuco, Northeast Brazil (Figure 1). The region is situated within the geographical coordinates of climatic transition, presenting a climate classified, according to Köppen, as As' (tropical rainy with dry summer). The orchard occupies an area of approximately 700 m^2, with trees approximately 13 years

old, maintained under standardized agronomic management, without the use of intensive irrigation systems during the experimental period. The study area comprises five star fruit genotypes developed by IPA's genetic improvement program. These genotypes, although not yet fully characterized morphologically, represent the genetic variability available in the region and are systematically distributed in the field to allow for cross-pollination.

Floral Biology and Phenology of Anthesis

For the characterization of floral biology, 18 plants of uniform size were selected and randomly distributed throughout the orchard. Representative branches from different positions in the canopy were selected from each plant. In total, 183 flower buds in the pre-anthesis stage ("balloon" stage) were individually marked with colored cotton threads to allow daily monitoring without interfering with flower morphology. Observations were made visually by trained examiners at one-hour intervals, starting at 7:00 AM and ending at 5:00 PM. During this period, the total duration of the orchard's flowering and the individual longevity of each flower were monitored, from petal opening (anthesis) to wilting or corolla fall. Morphometric parameters were obtained using millimeter rulers and digital calipers, measuring the number of inflorescences per branch (standardized to 30 cm in length), the number of flowers per inflorescence, the total flower density per branch, and the average inflorescence length. This data is crucial for understanding the availability of resources to pollinators.

Dynamics of Stigmatistic Receptivity

A key indicator of the female reproductive readiness period was evaluated using histochemical methods. The peroxidase activity test with 3% hydrogen peroxide (H_2O_2) was used (Dafni et al., 2005). The experiment was designed to cover the flower's entire daily activity period, collecting 20 flowers at different stages of opening every hour from 7:00 AM to 5:00 PM. In the field laboratory, the peroxide was applied directly to the stigmatic surface using a dropper and observed under a stereoscopic magnifying glass. Receptivity was confirmed by the occurrence of immediate effervescence (formation of oxygen bubbles), indicating the enzymatic activity necessary for pollen grain germination. This procedure allowed the identification of the peak receptivity and its correlation with the time of greatest bee visitation.

Survey and Identification of Visiting Insects

The survey of visiting insects was carried out through direct observations in the treetops during full bloom. Sampling took place between 5:00 AM and 5:00 PM, aiming to capture visitors from the first twilight visitors until the end of their daily activity. The sampling effort consisted of 10-minute observation periods per hour, totaling 10 non-consecutive monitoring days, chosen under favorable weather conditions (no rain and moderate winds). During the observations, the insects were photographed and analyzed with the aid of hand magnifiers to record their foraging behavior. The visitors were categorized according to the resource sought: nectar

Fig 1. Area of a star fruit tree (*Averrhoa carambola* L.) orchard in Northeast Brazil.

Fig 2. Floral phenology up to initial fruit set in star fruit trees (*Averrhoa carambola* L.) in Northeast Brazil**.**

(when the bee inserted its glossa into the base of the corolla) or resin (when it scraped the floral pedicel or bract with the aid of its mandibles). Following behavioral observation, specimens were collected using handheld entomological nets, sacrificed in ethyl acetate or 70% alcohol chambers, and sent for mounting and taxonomic identification by specialists, serving as reference material for the study.

Foraging Pattern of Apis mellifera and Trigona spinipes

For the most abundant species, preliminarily identified as *A. mellifera* and *T. spinipes*, a detailed study of foraging patterns was conducted. Digital stopwatches were used to record the time each individual spent on a single flower and the total number of flowers visited per inflorescence before the bee left the plant or exited the observer's field of vision. These records allowed calculation of the visitation rate (flowers/minute) and assessment of whether the bees' behavior favored geitonogamous pollination (between flowers of the same plant) or cross-pollination (between different plants), a determining factor for reproductive success in self-incompatible species such as the star fruit tree.

Pollination Requirements Treatments

To investigate the crop's dependence on biotic agents and the role of wind, three distinct experimental treatments were established:

T1 – Free Pollination (Control) (Figure 3-A): A total of 823 flower buds were marked and kept exposed to all natural floral visitors. This treatment quantified the baseline reproductive success of the area under normal environmental conditions.

T2 – Self-pollination (Autogamy Control) (Figure 3-B): 788 buds in pre-anthesis were selected and isolated with waterproof paper bags before the flowers opened. The isolation

Fig 3. Pollination treatments in star fruit trees (*Averrhoa carambola* L.) in Northeast Brazil: (A) T1 - Open pollination treatment; (B) T2 - Self-pollination treatment; (C) T3 - Anemophilous pollination treatment; (D) Pollinator efficiency test with *Apis mellifera* L.

prevented the entry of any external agent, aiming to verify if the floral architecture of the star fruit tree allows for successful spontaneous self-pollination.

T3 – Anemophilous Pollination (Role of Wind) (Figure 3-C): 406 buds were isolated with muslin bags (fine mesh). This mesh allows air currents and wind-borne pollen to pass, but prevents access to bees and other pollinating insects. The objective was to isolate the contribution of anemophilous pollination to fruit production.

In all treatments, reproductive success (initial fruit set) was recorded five days after anthesis. This interval was defined as the period during which unfertilized flowers abscise, while fertilized ovaries exhibit a characteristic dilation, signaling the onset of fruit development.

Apis mellifera Pollinator Efficiency Test

To determine if a single visit by *A. mellifera* is sufficient to promote fertilization of star fruit, the "single visit" methodology was used (Figure 3-D). 254 pre-anthesis buds were isolated using muslin bags. The following day, after the flowers opened, the bags were temporarily removed. The flowers were intensively monitored until an *A. mellifera* worker bee made its first landing and effective contact with the reproductive structures (stigmas and anthers). Immediately after the bee left, the visited flower was tagged with the time and re-bagged to prevent subsequent visits. The fruit set resulting from this controlled visit was recorded 5 days later and statistically compared with the results of the open-pollination and self-pollination treatments.

Data Processing and Statistical Analysis

The data were organized in spreadsheets and subjected to rigorous statistical analysis using SAS (Statistical Analysis System) software. For morphometric and floral biology variables, the GLM (General Linear Model) procedure was used, suitable for handling unbalanced designs and sample variability. For fruit set data (binomial variables: 1 for success, 0 for failure), the FREQ procedure with the CHISQ option was applied. This allowed for Chi-square (χ^2) tests to determine whether the observed differences in pollination rates (Free, Restricted, Wind, and *Apis* Efficiency) were statistically significant. All analyses were conducted with a significance level of 5% ($\alpha = 0.05$).

Results

The flowering period of the star fruit trees spanned December to February, totaling approximately 90 days of available floral resources (Table 1). Phenological synchrony was observed among the individuals in the orchard, with all trees flowering simultaneously.

The inflorescences were organized in raceme panicles, located predominantly in the axils of mature leaves and on woody branches. The average length of the inflorescences was 7.8 ± 2.6 cm (n = 32). In terms of floral density, an average of 9.17 ± 2.79 inflorescences per 30 cm branch was recorded. Each inflorescence had, on average, 21.22 ± 11.36 flowers, resulting in a potential density of up to 199.56 ± 131.52 flowers per branch segment (30 cm). The duration of an inflorescence, from the emergence of the first bud to the senescence of the last flower, varied between 9 and 16 days.

The flowers of *A. carambola* are hermaphroditic, actinomorphic, and pentamerous, displaying coloration ranging from shades of white, pink, and purple. The floral structure consists of 5 petals, 5 sepals, 5 functional stamens, and 5 staminodes. The corolla is open, facilitating access to nectar and pollen. No fragrance perceptible to the human sense of smell was detected during any stage of anthesis.

Morphologically, the stigma is positioned ahead of the stamens in relation to the entry route of visitors. Floral development occurs acropetal (from the base to the apex of the inflorescence), allowing the coexistence of buds, open flowers, and developing fruits on the same branch.

Anthesis begins at 7:00 AM, with full corolla opening occurring around 8:00 AM. Floral longevity is ephemeral, limited to only one day (approximately 12 hours of exposure). The hydrogen peroxide test confirmed that the stigma remains receptive throughout the entire period the flower is open (7:00 AM to 5:00 PM), evidenced by the immediate effervescence on the stigmatic surface at all evaluated times. After effective pollination, initial fruit set was observed on the 5th day post-anthesis.

The insect fauna visiting the starfruit tree consisted of insects from the orders Hymenoptera, Diptera, and Lepidoptera, distributed among five families (Figure 4). The order Hymenoptera was the most representative, comprising two bee species (*T. spinipes* and *A. mellifera*), as well as unidentified wasps (Vespidae) and ants (Formicidae).

Bees (Apidae) were overwhelmingly predominant, accounting for 95.3% of the total eusocial individuals quantified (n = 3,228). Among all observed visitors, *T. spinipes* was the most abundant species, representing 58.3% of the total sample (1,975 individuals), followed by *A. mellifera* with 37% (1,253 individuals) (Figure 5). The remaining species, combined, totaled only 4.7% of the visit frequency (Figure 5).

Table 1. Characteristics of floral biology in star fruit trees (*Averrhoa carambola* L.) in Northeast Brazil.

Characters	*Averrhoa carambola* L.
Flowering duration	3 months
Flower longevity	1 day
Duration of the inflorescence with flowers	9 to 16 days
Previous time	7-8 hours
Number of inflorescences per branch	9,17 ± 2,79
Number of flowers per inflorescence	21,22 ± 11,36
Number of flowers per branch	199,56 ± 131,52
Stigma receptivity	7 to 17 hours
Odor production	No

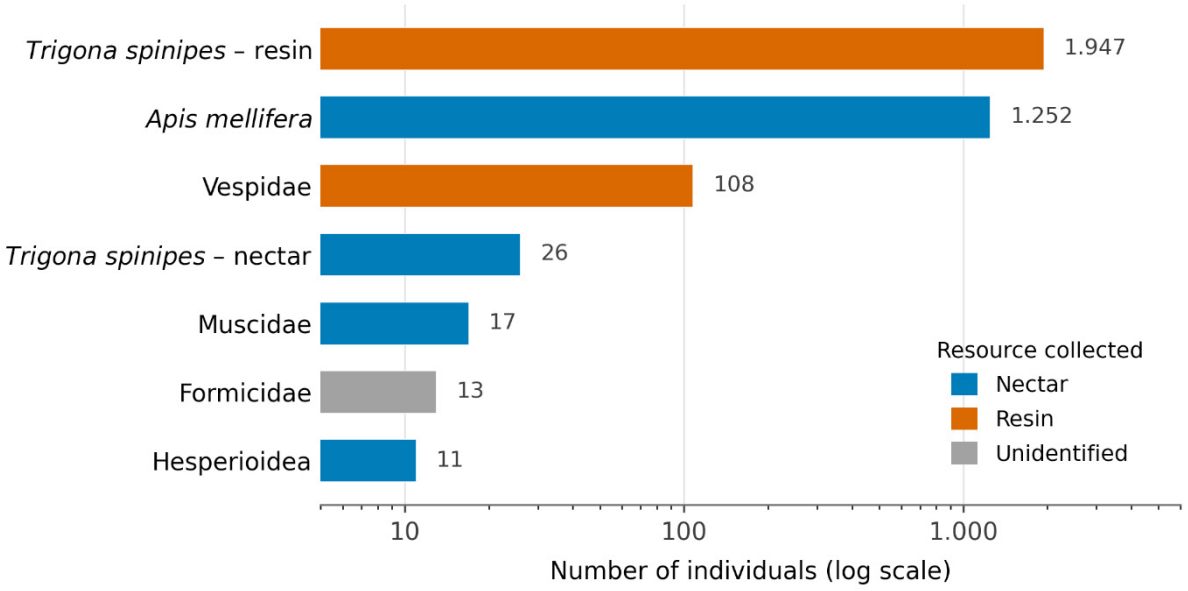

Fig 4. Number of individuals and resources collected from star fruit flowers (*Averrhoa carambola* L.) during 10 non-consecutive monitoring days in Northeast Brazil.

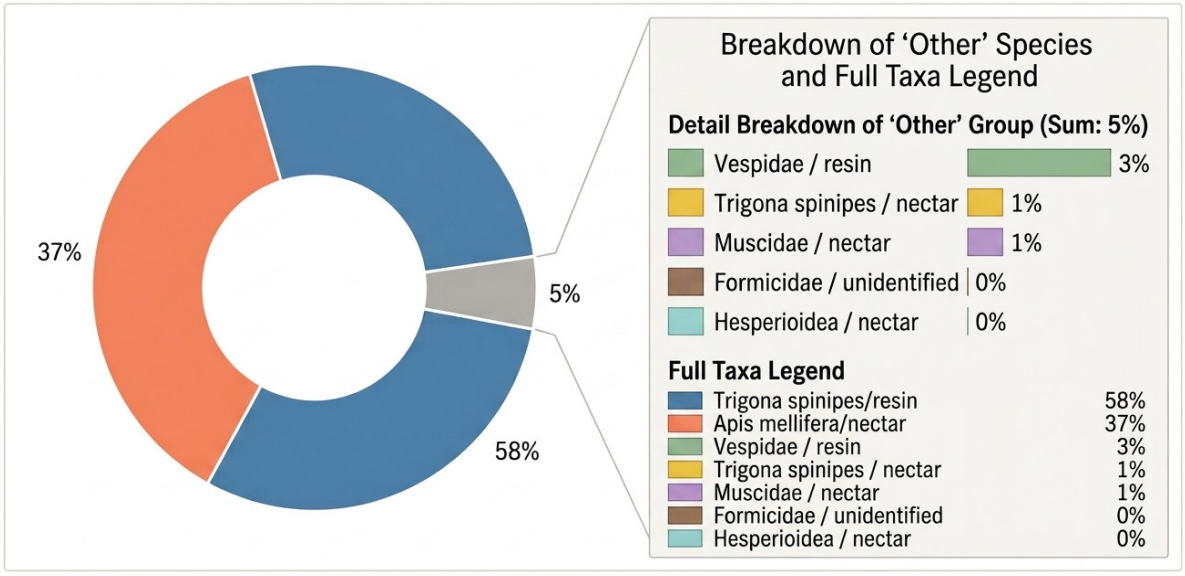

Fig 5. Percentage of individuals and resources collected from star fruit flowers (*Averrhoa carambola* L.) during 10 non-consecutive monitoring days in Northeast Brazil.

Regarding floral resources, nectar was the main attractant for most insects. However, a distinct behavior was observed in *T. spinipes* and Vespidae: the vast majority of *T. spinipes individuals* (n = 1,947) were recorded collecting resin or exudates from the floral pedicel and bracts (Figure 6-A), while only a small portion (n = 28) focused on nectar collection (Figure 6-B). The same pattern of resin preference was observed for Vespidae representatives (Figure 7-A). Visitors from the Muscidae, Formicidae (Figure 7-B), and Hesperioidea families showed low visitation frequency, focusing exclusively on nectar or only exploring the floral structure.

The foraging activity of floral visitors in the starfruit orchard occurred throughout the observation period, from 5:00 AM to 5:00 PM. It was found that the most abundant species, *T. spinipes* and *A. mellifera*, exhibited distinct temporal and resource-preference patterns (Figure 8).

T. spinipes (resin collectors) began their activities early at 05:00, before anthesis, reaching peak resin collection at 07:00 with approximately 32 individuals recorded. After this peak, activity gradually decreased, ending around 17:00 (Figure 8). *T. spinipes* (nectar collectors) collected this resource significantly less and later, starting at 07:00 and remaining at low and stable levels throughout the day, with a slight

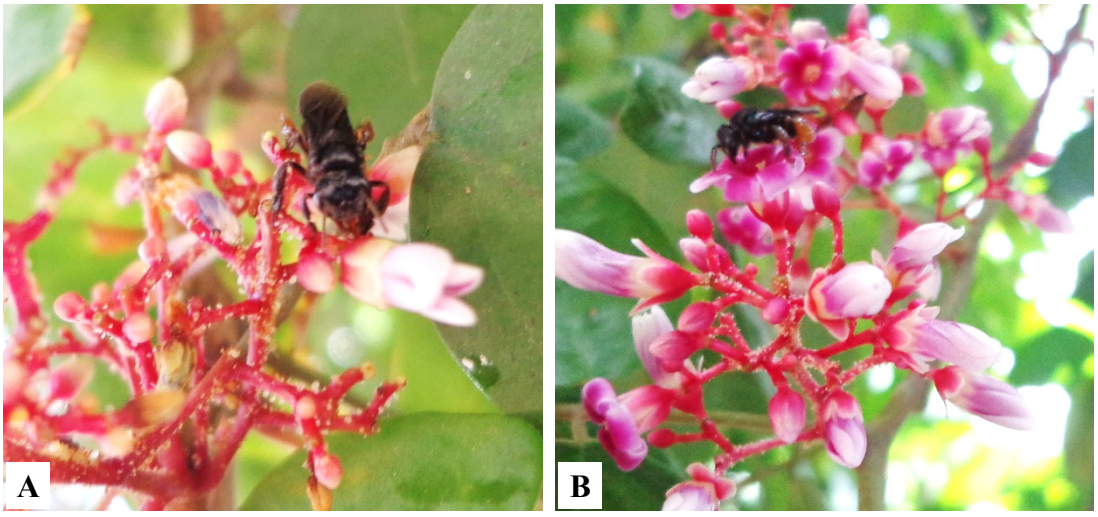

Fig 6. *Trigona spinipes* on star fruit flowers (*Averrhoa carambola* L.): (A) Collecting resin on the pedicel of closed flowers; (B) Collecting nectar.

Fig 7. Floral visiting insects of the star fruit tree (*Averrhoa carambola* L.): (A) Wasp collecting resin on the pedicel of closed flowers; (B) Ant exploring flowers.

increase (peak) at 15:00 (Figure 8). Meanwhile, *A. mellifera* began foraging only at 07:00, coinciding with floral anthesis. The number of foragers progressively increased to a peak of about 25 at 11:00, then gradually decreased and ceased completely after 17:00 (Figure 8). This species collected nectar exclusively.

The analysis of foraging patterns focused on the two most abundant species that used nectar as a resource: *A. mellifera* (37% of total visits) and *T. spinipes* (only 1.4% of visits for nectar). There were statistically significant differences ($p < 0.05$) in all visitation time and rhythm variables between the two species (Table 2).

Table 2. Foraging pattern of two bee species visiting the star fruit tree (*Averrhoa carambola* L.) in Northeast Brazil.

Variables	Species			
	Apis mellifera		*Trigona spinipes*	
	n	X ± σ	n	X ± σ
Time spent on the flower (seconds)	25	4,26 ± 0,58 b	18	24,64 ± 7,70 a
Time spent on the inflorescence (seconds)	18	5,36 ± 1,40 b	13	36,92 ± 10,18 a
Flowers/minute	20	10,15 ± 1,28 a	16	4,69 ± 1,40 b
Inflorescence/minute	22	8,5 ± 2,95 a	17	4,47 ± 0,92 b
Time on flower buds (seconds)	11	9,33 ± 0,52	-	-

Means in rows followed by different letters differ significantly from each other ($p < 0.05$).

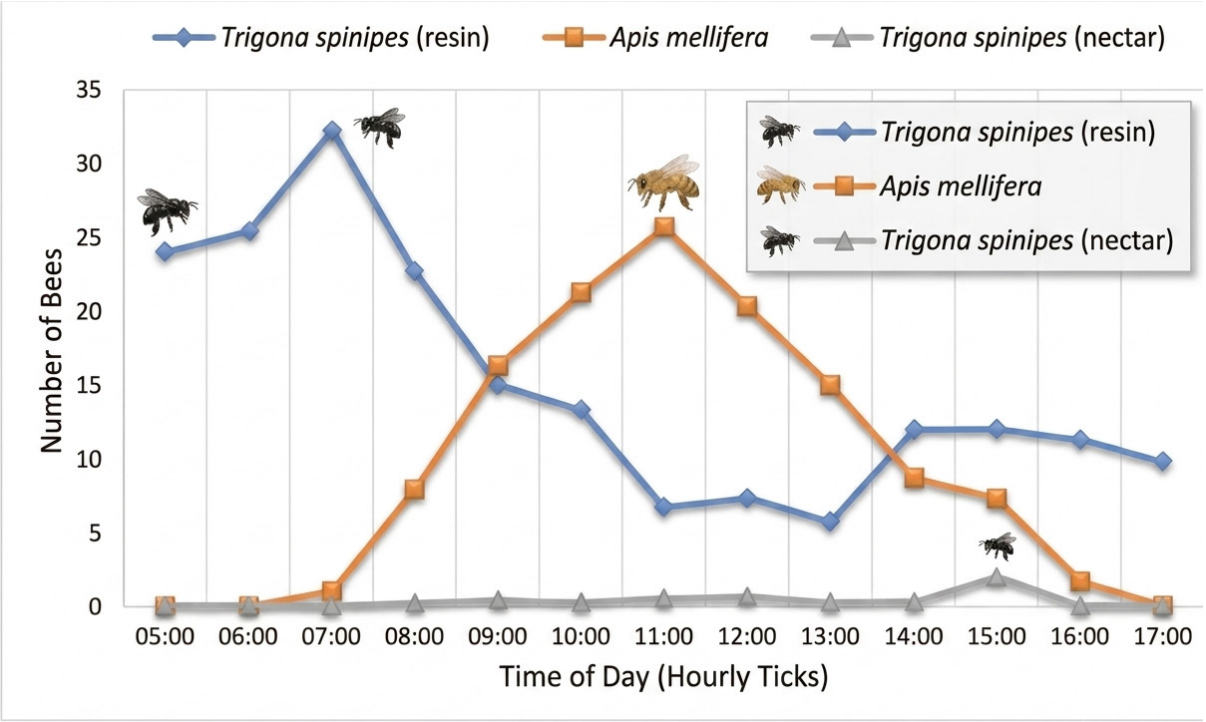

Fig 8. Times, resource collected, and number of bees grazing on star fruit trees (*Averrhoa carambola* L.) during 10 non-consecutive monitoring days in Northeast Brazil.

The worker ants of *A. mellifera* exhibited a significantly faster collection rate, remaining on average 4.26 ± 0.58 seconds per flower, while *T. spinipes* spent 24.64 ± 7.70 seconds on the same activity. This agility was reflected in the visitation rate: *A. mellifera* visited 10.15 ± 1.28 flowers per minute, a value significantly higher than the 4.69 ± 1.40 recorded for *T. spinipes.*

Regarding the exploration of inflorescences, *A. mellifera* spent an average of 5.36 ± 1.40 seconds per inflorescence and visited 8.5 ± 2.95 inflorescences per minute. In contrast, *T. spinipes* remained 36.92 ± 10.18 seconds on each inflorescence, visiting only 4.47 ± 0.92 per minute. Additionally, foraging behavior on flower buds (pre-anthesis) was recorded by *A. mellifera*, with an average handling time of 9.33 ± 0.52 seconds.

The star fruit tree (*Averrhoa carambola* L.) showed fruit formation in all pollination treatments tested, indicating the ability to produce fruit under different pollination conditions. However, there was a statistically significant difference ($p < 0.05$) among all evaluated methods (Table 3).

Directed pollination by *A. mellifera* (T4) obtained the highest initial fruit set rate (3.1%), significantly exceeding all other treatments. Free pollination (T1) showed the second-best performance (1.9%), followed by restricted pollination with muslin bags (T3) (1.2%). The lowest fruit set rate was observed in the treatment with paper bags (T2), where only 0.5% of the buds turned into fruits (Table 3).

Discussion

The phenological dynamics observed in the star fruit tree (*Averrhoa carambola*), characterized by a broad three-month flowering period and remarkable synchrony among individuals, reveal an evolutionary strategy aimed at maximizing attractiveness on a landscape scale. Intraspecific synchrony is a critical factor for allogamous tropical plants. According to the "mass flowering" hypothesis discussed by Rocca and Sazima (2006), the collective visual display acts as a long-distance signal, creating a "market effect" that increases the

Table 3. Initial fruit set of the star fruit tree (*Averrhoa carambola* L.) under different forms of flower pollination in Northeast Brazil.

Treatments	Number of flower buds	Number of fruits that set	Initial fruit set rate (%)
T1 - Open pollination	823	16	1,9 b
T2 - Restricted pollination with paper bags	788	4	0,5 d
T3 - Restricted pollination with muslin bags	406	5	1,2 c
T4 - Pollination by *Apis mellifera*	254	8	3,1 a

Values in the column followed by different letters differ significantly from each other ($p < 0.05$).

probability of visitation by generalist pollinators. For self-incompatible species, or those with mechanisms that hinder self-pollination, as is the case with the star fruit tree, this synchrony is not only advantageous but vital, as it ensures the overlap of phenological phases between pollen donors and recipients, thereby facilitating exogenous gene flow.

The floral morphology of the star fruit tree reinforces this generalist pollination syndrome. The open corolla structure, contrasting colors (lilac petals with an albino center), and the absence of severe morphological restrictions (such as deep spurs) indicate an adaptation to allow access to a wide guild of visitors. According to Richards (1986), flowers with these "promiscuous" characteristics evolved to exploit the diversity of insects available in the environment, a safety strategy in habitats where the abundance of specific pollinators can fluctuate. The attraction, in this case, seems to be predominantly visual, given the absence of odor perceptible to humans, suggesting that visual cues (nectar guides and spectral contrast) are the beginnings of insect orientation at short distances.

Physiologically, the evidence of constant stigma receptivity throughout the day, as indicated by peroxidase activity (Dafni, 2005), suggests that the plant maintains an extended "window of opportunity." This is ecologically costly for the plant (maintaining living, active tissues consumes energy), but evolutionarily rewarding, as it allows visits at both the peak of the morning and the end of the afternoon to result in fertilization.

One noteworthy agronomic finding is the precocity of initial fruit set, observed as early as the 5th day, contrasting with the 7 to 10 days interval classically reported by Knight (1965). This phenological acceleration should not be seen as an isolated event but interpreted in light of climate change and the edaphoclimatic conditions of the semi-arid/northeastern region of Brazil. Higher average temperatures and intense solar radiation tend to accelerate plant metabolic rates, shortening the initial embryonic development phases.

The composition of the floral visitor community (n = 6) reflects a scenario of ecological simplification. Although the taxonomic diversity finds parallels with studies in the Amazon region (Cabreira et al., 2011), the observed community structure is typical of anthropized landscapes. The absolute predominance of only two eusocial species (*Trigona spinipes* and *Apis mellifera*) and the absence of large solitary bees (such as *Xylocopa* or *Centris*) or long-tongued bees corroborate the theory of "environmental filters".

As recently reviewed by Ferreira et al. (2024), surrounding agricultural matrices act as selective barriers. Habitat fragmentation, landscape homogenization, and the historical use of agrochemicals eliminate specialist species, which have restricted nesting requirements (exposed soil, dead wood) and diets. What remains are generalist and resilient species, capable of exploiting varied resources and flying long distances, typical characteristics of the genus *Apis* and *Trigona*.

The presence of ants and wasps, although classified as occasional visitors, adds a layer of complexity to the network of interactions. Ants, when patrolling the flowers, can act as "biological guards" against herbivores, but their role in pollination is limited by the secretion of antibiotic substances in the cuticle that can render the pollen unviable (facultative myrmecophily syndrome). Wasps, when searching for resin or prey, perform an accidental and inefficient transport of pollen, not comparable to the efficiency of bees. Therefore, the pollination of the star fruit tree in this system depends almost exclusively on the competitive or complementary interaction between *Apis* and *Trigona*.

The numerical dominance of these social bees (Free, 1993; Roubik, 1989) is due to their biology of "mass recruitment". Once a scout bee locates the abundant nectar source of the starfruit tree, which acts as a vital "resource plant" during periods of scarcity of native flora, it recruits hundreds of worker bees, saturating the environment. This saturation phenomenon is beneficial to the plant only if the visitor is efficient; otherwise, it can generate a high reproductive cost, as discussed below.

Behavioral analysis revealed a clear niche segregation and resource partitioning between the two dominant species, a central finding for understanding the crop's reproductive success. *T. spinipes*, despite representing 58.3% of the abundance, behaved functionally not as a pollinator, but as an exploiter of structural resources.

The focus of *T. spinipes* on collecting resin from the pedicel and bracts, rather than from intra-corolla floral resources, is an intriguing behavior. Bees of the genus *Trigona* have a high demand for plant resins for nest construction, sanitary defense, and colony sealing. The star fruit tree apparently offers a high-quality resinous exudate or easy access to these vegetative structures. By prioritizing resin, *Trigona* avoids contact with the anthers and stigma, making its visits reproductively neutral or nonexistent.

This result contrasts sharply with Asian literature. In Malaysia, *Trigona thoracica* is cited as an efficient pollinator (Phoon et al., 1984). This discrepancy highlights the importance of not generalizing pollination efficiency at the genus level; the interaction is species-specific and context-dependent. While recent global reviews, such as that of Malathi et al. (2025), highlight the growing potential of non-Apis bees (including stingless bees) for fruit quality in controlled environments (greenhouses), our field data show that, in open environments with resin availability, *T. spinipes* deviates from its ecological function, ceasing to act as a pollen vector.

This behavioral change validates the recent observations of Razo-León et al. (2025). The authors demonstrate that, in scenarios of environmental simplification and fragmentation, not only is there a loss of species, but also a modification of the feeding niches of the remaining species. *Trigona* shifted its focus to non-reproductive resources, while *Apis mellifera* occupied the dominant nectarivorous niche.

The efficiency of *Apis mellifera* in this system is explained by the "Optimal Foraging Theory". The high density of flowers and the large amount of nectar make the star fruit tree a high-return energy source. The behavior of *Apis* was

mechanically perfect for the flower: by inserting its proboscis at the base of the corolla to reach the nectary, the bee performs sternotribic pollination, where the pollen is deposited in the ventral region of the thorax and abdomen, the exact location of contact with the stigma in subsequent visits (Vaissière et al., 2011).

Even the "pittling" or forcing of flower buds by *Apis* (opening the flower before anthesis) can have positive systemic effects. According to the hypothesis of Maloof and Inouye (2000), nectar thieves can reduce the average reward per flower, forcing legitimate pollinators to visit more flowers and fly to other trees in search of resources, inadvertently increasing cross-pollen flow (reduced geitonogamy, increased xenogamy).

The quantitative comparison between the pollination treatments reveals a clear diagnosis: the orchard suffers from a pollination deficit. The concept of deficit, ecologically defined as insufficient pollen transfer that limits plant sexual reproduction (Smith et al., 2022), is evidenced here by the discrepancy between open pollination (T1: 1.9%) and directed pollination (T4: 3.1%).

The approximately 63% increase in fruit set provided by *A. mellifera* indicates that the natural ecosystem service ("free pollination") is operating well below its potential. In agronomic terms, this represents a "yield gap" that could be filled with management. The low rate of free pollination is a direct reflection of the inefficiency of *Trigona* (the most frequent visitor does not pollinate) and the dependence on a single efficient vector (*Apis*) whose natural population may not be sufficient to cover the massive flowering.

Isolation results (using paper bags and tulle) confirm dependence on biotic vectors. The extremely low fruit set (0.5%) in spontaneous self-pollination reinforces the role of herkogamy (spatial separation between the anther and the stigma) and, possibly, genetic self-incompatibility mechanisms, which are common in the Oxalidaceae family (Novo et al., 2021). Wind (anemophily) proved to be a secondary and unreliable vector (1.2%), incapable of sustaining commercial production.

It is crucial to situate these results within the current scientific debate. Recently, Abdullah et al. (2024) demonstrated, in studies with loofah (*Luffa*), that solitary bees can be more efficient than bees of the genus *Apis*. However, our results show that this rule is not universal. For the star fruit tree, under the conditions of Northeast Brazil, *Apis mellifera* is irreplaceable. This is probably due to floral morphology that favors bees with medium-long tongues and social behavior that enables rapid recruitment to exploit massive flowering, something solitary bees cannot achieve on the same scale. Therefore, while the conservation of solitary bees is vital globally, for the star fruit commodity, the management of *Apis* is the technical priority.

The practical conclusion of this study points to the need for further technological advancements in pollination. The introduction or maintenance of *A. mellifera colonies* in star fruit orchards should not be seen as an option, but as an essential agricultural input, just like irrigation or fertilization.

This recommendation aligns with global trends described by Sáez et al. (2022), who warn of the growing dependence of modern agriculture on pollination services. More specifically, the recent study by Yogapriya et al. (2025) empirically demonstrates that the introduction of Apis hives significantly increases productivity parameters in crops with nutrient deficiencies. For star fruit producers, this means that renting hives or integrated beekeeping can result in heavier, sweeter, and more abundant fruit.

However, this "pollinator monoculture" strategy (exclusive dependence on *Apis*) carries risks. The global population of managed beehives is growing more slowly than agricultural demand for pollination (Mashilingi, 2022), and bees face global health crises. Therefore, management must be integrated with landscape conservation.

The observed coexistence between *Apis* and *Trigona*, despite the latter's inefficiency as a pollinator, suggests that the environment still supports native populations. To preserve this balance and ensure the health of introduced colonies, phytosanitary management must be rigorous. According to IPBES guidelines (2016), the use of pesticides, especially neonicotinoids and broad-spectrum insecticides, should be banned during flowering.

Given the observed distribution of foraging activity, a "safety window" for agricultural applications is proposed. Since visitation activity is intensely concentrated between 7:00 AM and 4:00 PM, pesticide interventions, when strictly necessary and using molecules with low residual toxicity, should be carried out in the late afternoon or at night (Novo et al., 2021). This minimizes direct contact (knock-down effect) with both the efficient pollinator (*Apis*) and the native fauna (*Trigona*, wasps, ants), preserving the little functional biodiversity that still remains in productive agroecosystems.

In short, the productivity of star fruit trees in Brazil is at a delicate threshold, sustained almost solely by *Apis mellifera*. Strategies that integrate the supplementation of beehives with the conservation of forest fragments (to try to attract other pollinators and provide nesting sites) are the way to transform this simplified system into a more resilient and productive agroecosystem.

Conclusions

The star fruit tree (*Averrhoa carambola* L.) exhibits synchronous and massive flowering, but it is dependent on biotic vectors due to the ephemeral nature of its flowers and its morphology, which hinders spontaneous self-pollination, as demonstrated by the low fruit set in total isolation.

Although the *Trigona spinipes* is the most frequent visitor, its contribution to productivity is negligible, since its behavior focuses on collecting resin and exudates, without effective contact with the reproductive structures. In contrast, the honeybee *Apis mellifera*, despite being less abundant than *T. spinipes*, proves to be the most effective pollinator. Its high visitation rate and exclusive nectar-collecting behavior resulted in the highest initial success rate.

The results reveal a pollination deficit in the orchard, since pollination directed by *A. mellifera* significantly surpassed open pollination. Therefore, to maximize the agricultural yield of star fruit, it is essential to manage *A. mellifera* colonies, ensuring that the high floral density of the crop is efficiently converted into fruit.

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Authors' Contributions

CGSJP: conceptualization, methodology, investigation, formal analysis, data curation, writing-original draft, visualization.
MOM: conceptualization, methodology, resources, supervision, project administration, writing-review & editing.

References

Abdullah, S., Ali, M., Khan, F. Z. A., Sajjad, A., Qayyum, M. A. & Ahmad, N. (2024). Solitary Bees Are More Efficient Pollinators of Sponge Gourd than Giant Honeybees and Syrphid Flies. Sociobiology, 71: e10279. https://doi.org/10.13102/sociobiology.v71i3.10279

Aguilar, R., Cristóbal-Pérez, E. J., Márquez, V., Carbone, L. M., Paglia, I., Freitas, L., Ashworth, L., Martén-Rodríguez, S., Fernandes, G. W., Lobo, J., Fuchs, E. J. & Quesada, M. (2025). Anthropogenic land-use change decreases pollination and male and female fitness in terrestrial flowering plants. Annals of Botany, 135: 57-74. https://doi.org/10.1093/aob/mcae076

Ahsan, Z., Wu, Z., Lin, Z., Ji, T. & Wang, K. (2025). The sublethal effects of neonicotinoids on honeybees. Biology, 14: 1076.

Bastos, D. C. (2004). A cultura da carambola. Revista Brasileira de Fruticultura, 26: 193-384. https://doi.org/10.1590/s0100-29452004000200001

Cabreira, D. M. B., Biondo, P. L. T. A., Bezerra, T. M., Trindade, T. A., Ribeiro, J. E. S. & Kaminski, A. C. (2011). Visitantes florais de carambola, *Averrhoa carambola* L. (Oxalidaceae) na região do Médio Solimões, Amazonas, Brasil. In: 63ª Reunião Anual da Sociedade Brasileira para o Progresso da Ciência.

Dafni, A., Kevan, P. G. & Husband, B. C. (2005). Practical pollination biology. Cambridge, MA: Enviroquest Ltd.

Dicks, L. V., Breeze, T. D., Ngo, H. T., Senapathi, D., An, J., Aizen, M. A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L. A., Gemmill-Herren, B., Howlett, B. G., Imperatriz-Fonseca, V. L., Johnson, S. D., Kovács-Hostyánszki, A., Kwon, Y. J., Lattorff, H. M. G., Lungharwo, T., Seymour, C. L., Vanbergen, A. J. & Potts, S. G. (2021). A global-scale expert assessment of drivers and risks associated with pollinator decline. Nature Ecology and Evolution, 5: 1453-1461. https://doi.org/10.21203/rs.3.rs-90439/v1

Donadio, L. C., Silva, J. A. A., Araújo, P. R. S. & Prado, R. M. (2001). Caramboleira (Averrhoa carambola L.). Jaboticabal: Sociedade Brasileira de Fruticultura.

Ellis, R. A., Weis, T., Suryanarayanan, S. & Beilin, K. (2020). From a free gift of nature to a precarious commodity: Bees, pollination services, and industrial agriculture. Journal of Agrarian Change, 20: 437-459. https://doi.org/10.1111/joac.12360

Ferreira, J. V. A., Morante-Filho, J. C., Somavilla, A., Storck-Tonon, D. & Benchimol, M. (2024). Effect of Agricultural Matrices on the Biodiversity Metrics of Bees (Hymenoptera: Anthophila): A Review. Sociobiology, 71: e11410. https://doi.org/10.13102/sociobiology.v72i3.11410

Free, J. B. (1993). Insect pollination of crops (2. ed.). London: Academic Press.

Gallai, N., Salles, J. M., Settele, J. & Vaissière, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecological Economics, 68: 810-821. https://doi.org/10.1016/j.ecolecon.2008.06.014

Gao, Y. (2025). Pollination Biology: From Pollinators and Floral Traits to Landscape Management. Biology, 14: 1420. https://doi.org/10.3390/biology14101420

Gazzoni, D. L., Hoffmann-Campo, C. B., Zocolo, G. J. & Fernandes, M. C. (2025). Pollination as an ecosystem service in soybean production for climate change mitigation. Pesquisa Agropecuária Brasileira, 60: e04108. https://doi.org/10.1590/s1678-3921.pab2025.v60.04108

Giannini, T. C., Boff, S., Cordeiro, G. D., et al. (2015b). Crop pollinators in Brazil: a review of reported interactions. Apidologie, 46: 209-223. https://doi.org/10.1007/s13592-014-0316-z

Giannini, T. C., Boff, S., Cordeiro, G. D., Freitas, B. M., Saraiva, A. M., & Imperatriz-Fonseca, V. L. (2015a). The dependence of crops for pollinators and the economic value of pollination in Brazil. Journal of Economic Entomology, 108: 849-857. https://doi.org/10.1093/jee/tov093

IBGE (2025). Contribuição dos polinizadores para as produções agrícola e extrativista do Brasil: 2023. Rio de Janeiro: Instituto Brasileiro de Geografia e Estatística. https://doi.org/10.32385/rpmgf.v39i3.13835

IPBES. (2016). History of the establishment of IPBES. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Available at: https://www.ipbes.net/history-establishment.

Knight Jr., R. J. (1965). Heterostyly and pollination in carambola. Proceedings of the Florida State Horticultural Society, 78: 375-378.

Knight Jr., R. J. (1982). Partial loss of self-incompatibility in 'Golden Star' carambola. HortScience, 17: 72.

Malathi, J., Preetha, G., Saminathan, V. R., Keerthana, B., Kavitha, M., Prabu, P. C. & Pradeep, S. (2025). Pollination Redefined: Non-Apis B ees i n G reenhouse T omatoes and Emerging Global Research Trends. Sociobiology, 72: e11524. https://doi.org/10.13102/sociobiology.v72i3.11524

Maloof, J. E. & Inouye, D. W. (2000). Are nectar robbers cheaters or mutualists? Ecology, 81: 2651-2661. https://doi.org/10.1890/0012-9658(2000)081[2651:anrcom]2.0.co;2

Mashilingi, S. K., Shang, H., Garibaldi, L. A. & An, J. (2022). Honeybees are far too insufficient to supply optimum pollination services in agricultural systems worldwide. Agriculture, Ecosystems & Environment, 335: 108003. https://doi.org/10.1016/j.agee.2022.108003

Milfont, M. O., Rocha, E. E. M., Lima, A. O. N. & Freitas, B. M. (2013). Higher soybean production using honeybee and wild pollinators, a sustainable alternative to pesticides and autopollination. Environmental Chemistry Letters, 12: 412. https://doi.org/10.1007/s10311-013-0412-8

Novo, R. R., Almeida, N. M., Sá, T. F. F., Ferraz, L. G. B., Araújo, E. L. & Castro, C. C. (2021). Crop yield mediated by honeybees in a star fruit orchard exhibiting atypical distyly. Acta Botanica Brasilica, 35: 486-490. https://doi.org/10.1590/0102-33062020abb0373

Oliveira, W., Cruz-Neto, O., Silva, J. L. S., Tabarelli, M., Peres, C. A. & Lopes, A. V. (2025). Climate change will lead to local extinctions and mismatched range contractions disrupting bee-dependent crop pollination. Frontiers in Bee Science, 3: 1510451. https://doi.org/10.3389/frbee.2025.1510451

Peng, S., Ellison, A. M. & Davis, C. C. (2025). Climate change intensifies plant-pollinator mismatch and increases secondary extinction risk for plants in northern latitudes. Proceedings of the National Academy of Sciences of the United States of America, 122: e2506265122. https://doi.org/10.32942/x2vh1x

Phoon, A., Suhaimi, A. & Marshall, A. (1984). The pollination of some Malaysian fruit trees. In: 1st Simposium Biologi Kebangsaan (p. 87-111). Selangor Malaysia: Bangi.

Potts, S. G., Imperatriz-Fonseca, V. & Ngo, H. T. (Ed.). (2017). The assessment report on pollinators, pollination and food production of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Rasmussen, C. (2008). Molecular phylogeny of stingless bees: Insights into divergence times, biogeography, and nest architecture evolution. PhD Dissertation, University of Illinois at Urbana-Champaign. 301p.

Ray, P. K. (2002). Breeding tropical and subtropical fruits. Berlin: Springer-Verlag.

Razo-León, A. E., Huerta-Martínez, F. M., Becerra-Chiron, I. M., Jacobo-Pereira, C., Neri-Luna, C., Araujo-Alanis, L. & Muñoz-Urias, A. (2025). Habitat Fragmentation on Bee (Hymenoptera: Apoidea) Diversity, Food Niches, and Bee-Plant Interaction Networks. Diversity, 17: 834. https://doi.org/10.3390/d17120834

Richards, A. J. (1986). Plant breeding systems. London: Cambridge University Press.

Rocca, M. A. & Sazima, M. (2006). The dioecious, sphingophilous species *Citharexylum myrianthum* (Verbenaceae): pollination and visitor diversity. Flora, 201: 440-450. https://doi.org/10.1016/j.flora.2006.02.001

Roubik, D. W. (1989). Ecology and natural history of tropical bees. Cambridge: Cambridge University Press.

Sáez, A., Aguilar, R., Ashworth, L., Gleiser, G., Morales, C. L., Traveset, A. & Aizen, M. A. (2022). Managed honeybees decrease pollination limitation in self-compatible but not in self-incompatible crops. Proceedings of the Royal Society B - Biological Sciences, 289: 20220086. https://doi.org/10.1098/rspb.2022.0086

Smith, M. R., Mueller, N. D., Springmann, M., Sulser, T. B., Garibaldi, L. A., Gerber, J., Wiebe, K. & Myers, S. S. (2022). Pollinator deficits, food consumption, and consequences for human health: a modeling study. Environmental Health Perspectives, 130: 127003. https://doi.org/10.1289/ehp10947

Vaissière, B. E., Freitas, B. M. & Gemmill-Herren, B. (2011). Protocol to detect and assess pollination deficits in crops: a handbook for its use. Rome: FAO. https://doi.org/10.17504/protocols.io.pz7dp9n

Yogapriya, A., Usharani, B. & Suresh, K. (2025). Pollination Efficiency of the Indian Bee, Apis cerana indica Fab. in Bitter Gourd in Tamil Nadu, India. Sociobiology, 72: e11385. https://doi.org/10.13102/sociobiology.v72i4.11385

Zattara, E. E. & Aizen, M. A. (2021). Worldwide occurrence records suggest a global decline in bee species richness. One Earth, 4: 114-123. https://doi.org/10.1101/869784