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Cover: Fish species recorded in the Gowthami-Godavari Estuary, Andhra Pradesh: *Lutjanus johnii* (top left), *Triacanthus biaculeatus* (top right), *Acentrogobius cyanomos*, *Elops machnata*, *Trypauchen vagina*, *Oxyurichthys microlepis*. © Paromita Ray.



Zoophily and nectar-robbing by sunbirds in *Gardenia latifolia* Ait. (Rubiaceae)

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Abstract: *Gardenia latifolia* is a semi-deciduous tree species which blooms during the dry season. Its flowers are hermaphroditic, strongly fragrant, nectariferous, and specialized with a narrow corolla tube and concealed deep seated nectar. Thrips act as resident pollinators while bats and carpenter bees act as non-resident pollinators. Sunbirds act as nectar robbers and have no role in pollination. The flowers are milky white and fragrant on days 1 and 2; they cease fragrance and change color to golden yellow on day 3. Bats visit newly open, day 1 fragrant flowers for pollen collection while thrips use day 1 and day 2 flowers. Carpenter bees and sunbirds visit only day 2 flowers. The flower visiting activity of all these foragers indicates that they do not visit non-fragrant, golden yellow colored flowers although they possess nectar. Fruit is an indehiscent berry with seeds placed in pulp inside; the birds are the most likely seed dispersal agents when they break the pericarp and feed on the fruit pulp.

Keywords: Bats, carpenter bees, *Cochlospermum religiosum*, *Croton scabiosus*, evening anthesis, hermaphroditism, *Maerua apetala*, *Mylabris phalerata*, pollination, thrips.

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INTRODUCTION

In Rubiaceae, *Gardenia* is one of the largest genera (Davis et al. 2009) with 142 species of evergreen shrubs and small trees distributed in tropical and subtropical regions of Africa, Asia, Madagascar, Australasia, and Oceania (Puttock 1988). It includes a number of well known widely cultivated horticultural species for their fragrant flowers (Smith 1974). This genus is characterized by hermaphroditic flowers, often large and showy with corolla lobes overlapping to the left, pollen in tetrads, 1-locular ovaries with two to many parietal placentas, and fruits with numerous lenticulate seeds (Rakotonirina et al. 2012). Despite the wide distribution of this genus in tropical belts and the value of its species in horticulture due to their floral fragrance, there are no systematic studies on the reproductive ecology of any species. However, there are sporadic reports on the pollinators of three *Gardenia* species, *G. tubifera*, *G. jasminoides* and *G. thunbergia*. Freeman et al. (1991) reported that *G. tubifera* is possibly pollinated by moths. Okomoto et al. (2008) reported that *G. jasminoides* is typically a hawk-moth pollinated species in Japan. Johnson et al. (2017) reported that the African shrub, *Gardenia thunbergia* is pollinated exclusively by the convolvulus hawk moth, *Agrius convolvuli*. Reddy et al. (2021) reported that *G. latifolia* commonly known as Indian Boxwood is a small deciduous tree with dense foliage. It occurs in all deciduous forests of India. Its stem, bark and fruit are used in the treatment of skin diseases, stomach pain & snake bite in humans, and ephemeral fever in live stock; its fruit is used for making perfume. Despite its common occurrence and traditional economical values, it has not been investigated for its pollination ecology which is very important to understand its sexual reproduction and its association with local pollinator fauna. With this backdrop, the present study was aimed at carrying out field studies on the pollination ecology of *G. latifolia* Ait. to know whether this species is also pollinated by hawk moths or other flower visiting insects or animals. Further, whether its long tubular hypocarteriform flowers with deeply seated nectar facilitates foraging visits by flower visitors to collect forage illegitimately and if so, what would be the role of illegitimate nectar robbing on plant fitness in dry deciduous ecosystem of Idupulapaya Reserve Forest, Kadapa District, Andhra Pradesh, India.

MATERIALS AND METHODS

Gardenia latifolia Ait. trees at Idupulapaya Reserve Forest representing rocky, rugged terrain with deciduous forest ecosystem (14.33 °N 78.51 °E, 273 m) in Kadapa District, Andhra Pradesh, India, were selected for study during February–May 2021. During this period, the tree species, *Croton scabiosus* Bedd. (Euphorbiaceae), *Cochlospermum religiosum* (L.) Alston (Cochlospermaceae), *Maerua apetala* (Roth) M. Jacobs (Capparaceae) and *Gardenia latifolia* Ait. (Rubiaceae) were found blooming simultaneously. Of these, the first two species bear new foliage during the flowering phase while the third species is completely leafless during the flower phase. In the Indian Boxwood, *G. latifolia*, the flowering phase is initiated at the fag end of leaf fall but peak flowering occurs when complete leaf flushing occurs (Image 1a,b). Further, *C. scabiosus* and *G. latifolia* trees with scattered distribution are present in considerable numbers while the other tree species consisting of a few individuals are present here and there. The floral aspects were carefully observed and recorded for the characteristic traits of *G. latifolia*. Twenty maturing buds were tagged and followed for recording the time of anthesis and anther dehiscence. The same buds were followed at random for the growth and protrusion of style and stigma in relation to the level of dehisced anthers through corolla tube to record whether secondary pollen presentation mechanism is functional or not because this mechanism is the rule in the Rubiaceae family. Further, the important floral traits of the other simultaneously blooming tree species were also noted. Nectar volume of *G. latifolia* was measured using a graduated pipette while its sugar concentration was recorded using a hand sugar refractometer (Erma, Japan); twenty flowers were used for recording these two aspects. For the analysis of sugar types, paper chromatography method described by Harborne (1973) was followed. Nectar was placed on Whatman No. 1 of filter paper along with standard samples of glucose, fructose and sucrose. The paper was run ascendingly for 24 hours with a solvent system of n-butanol-acetone-water (4:5:1), sprayed with aniline oxalate spray reagent and dried at 120 °C in an electric oven for 20 minutes for the development of spots from the nectar and the standard sugars. Then, the sugar types present were recorded.

The flower visitors were observed on five sunny days of the flowering season for their flower approaching, probing and forage collection behaviour. The foraging activity was observed from sunrise to sunset to record the flower-visiting schedules of diurnal foragers and of

bats from 1700 h to 0500 h. The field methods described in Dafni et al. (2005) were followed for the collection of data on foraging visits, foraging schedule, foraging mode and flower handling time. The number of foraging visits made by each diurnal foraging species was recorded for 10 minutes at each hour throughout the day between 0600 h and 1800 h on five different days. Based on these visits, the mean number of total foraging visits made per day was calculated. The foraging mode employed for forage collection was also recorded while the foragers were probing the flowers. The time spent for probing and collecting the floral reward by each forager species was counted in seconds by using a stop watch; the number of observations made were according to the foraging visits made to the flowers during observation period. Based on the data, the mean time for handling flowers to collect the forage by each forager species was calculated to understand the flower to flower mobility rate. Among the flower visitors, sunbirds were found to exhibit nectar robbing behaviour; this behaviour was carefully observed with reference to its role in effecting pollination rate negatively or positively. The flower morphological characters were also noted to evaluate their specialized traits that contribute to the exploitation by nectar robbing sunbirds. Further, the observations on the foraging activity of the forager species visiting *G. latifolia* on other tree species simultaneously blooming

in the same area were also made to note whether they were resorting to display illegitimate or legitimate foraging behaviour to collect nectar. Fruit and seed characters were also described.

OBSERVATIONS

Gardenia latifolia is a medium-sized semi-deciduous tree with grey to light brown colored exfoliating bark displaying smooth, concave and rounded depressions. The leaves are oval to obovate, smooth and arranged opposite to each other or in whorls with very short stalks. Flowers are solitary, sessile, 5 cm long, extremely fragrant, hermaphroditic and appear at the end of branches. The calyx is bell-shaped with five valvate lobes apically. The corolla is hypocrateriform with a narrow tube and flaring suddenly into a flat arrangement of five obliquely obovate petals which are about half as long as the corolla tube. The stamens are five, epipetalous, placed at the throat of the corolla tube; the anthers are ditheous and dehisce by longitudinal slits. The style springs up from the center of the flower, runs parallel to corolla tube and gradually protrudes out of the corolla tube. The stigma is 5-lobed, green, club-shaped, thick and fleshy (Image 1h). Fruit is a 3–5 cm long globose indehiscent berry with crowned calyx lobes and consists

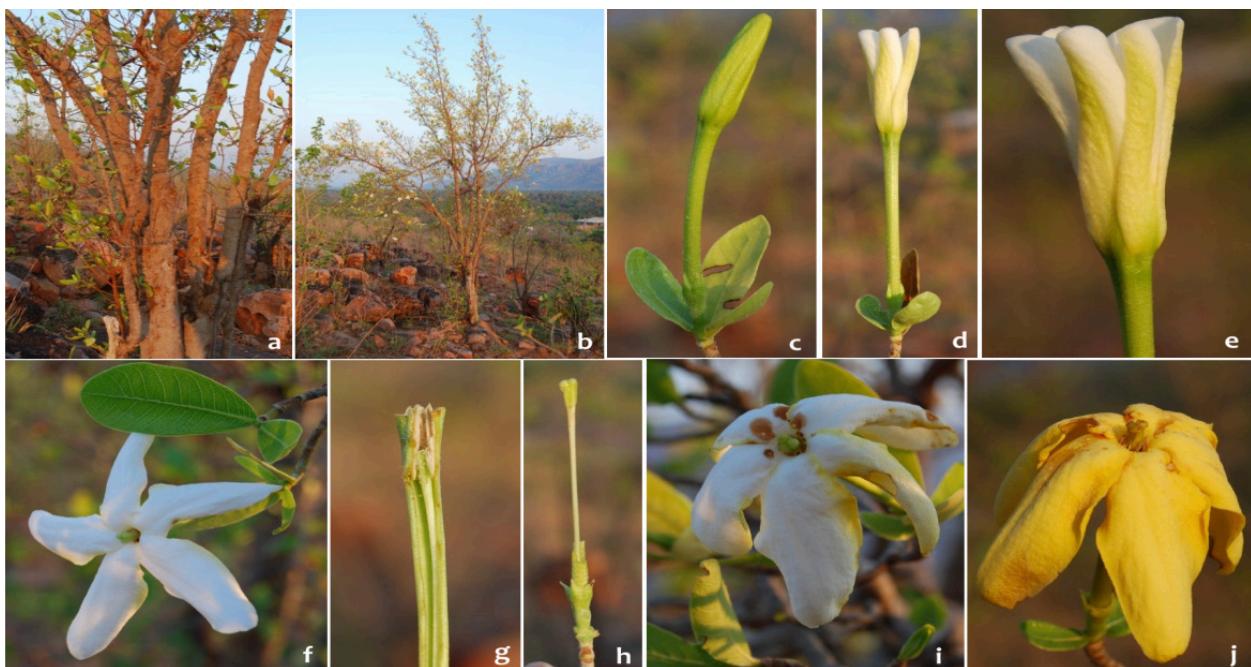


Image 1. *Gardenia latifolia*: a—Trunk | b—Leaf flushing and flowering | c—f—Anthesis stages | g—Anther dehiscence by longitudinal slits in bud stage (stigma below the height of anthers) | h—Pistil | i—Brown marks on the corolla indicating bat visit to the flower | j—3rd day flower.
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Table 1. List of foragers visiting the flowers of *Gardenia latifolia*.

Order	Family	Insect species	Foraging period (h)	No. of foraging visits/day# (N = 5 days)	Mode of foraging	Forage sought	Flower handling time (in seconds)
Hymenoptera	Apidae	<i>Xylocopa pubescens</i> *	0700–1200 Peak activity: 0900–1200	42 ± 5.3	Legitimate	Pollen	3.2 ± 0.08 (n = 42)
		<i>Xylocopa latipes</i> *	0700–1200 Peak activity: 0900–1200	39 ± 3.5	Legitimate	Pollen	2.8 ± 0.05 (n = 37)
Thysanoptera	Thripidae	Unidentified	0800–1700	Forages continuously	Legitimate	Pollen + Nectar	--
Passeriformes	Nectariniidae	<i>Nectarinia asiatica</i> **	0700–1600	53 ± 3.2	Illegitimate	Nectar	2.3 ± 0.8 (n = 31)
		<i>Nectarinia zeylonica</i> **	0700–1600	41 ± 2.2	Illegitimate	Nectar	2.6 ± 1.4 (n = 36)
Chiroptera	Pteropodidae	<i>Pteropus medius</i>	1830–0300	32 ± 3.7 (approx.)	Legitimate	Pollen	1.4 ± 0.8 (n = 27)

#No. of flowers under observation: Approximately 125 each day on a different tree.
*Collecting pollen from *Cochlospermum religiosum* and nectar from *Maerua apetala* legitimately.
**Collecting nectar from *Maerua apetala* legitimately and larvae of an unidentified local butterfly from the leaves of *Croton scabiosus*.

of many rugose seeds enclosed by pulp inside (Image 2h).

G. latifolia mature buds begin to open by 1600 h and are fully open by 1830 h (Image 1c–f). The flowers either stand erect or oriented slightly horizontally. The anthers dehisce about an hour prior to anthesis and each anther produces copious amount of fertile pollen (Image 1g). At anther dehiscence time, the stigma is placed below the height of the anthers but it gradually protrudes out of the corolla tube through the dehisced anthers at anthesis and in this process, the stigma is partially coated with self-pollen facilitating the occurrence of autonomous self-pollination. The stigma attains receptivity about an hour after flower-opening and extends its receptivity until the evening of the next day with peak receptivity from 1930 h to 1100 h on the next day. The corolla is milky white emitting strong sweet fragrance immediately after anthesis but it gradually fades losing fragrance simultaneously by the evening of the next day of anthesis. Then, the corolla appears golden yellow and turns light brown then withers and wilts on the 3rd day. The corolla together with stamens, style and stigma fall off gradually on 4th day while the calyx is persistent and provides protection to the apical part of the ovary with fertilized ovules throughout fruit growth, development, and maturation.

G. latifolia flowers initiate nectar secretion by nectaries at the base of the ovary during bud stage and its secretion ceases by the time of anthesis. Individual flowers produce 3.7 ± 0.76 µl of sucrose-rich nectar with $28.7 \pm 2.5\%$ total sugar concentration. The nectar remained in place throughout the flower life if not utilized by flower visitors. Field observations showed

that the flower-visitors made visits to day-1 and day-2 flowers only despite the availability of nectar in day-3 and 4 flowers.

Mature buds showed different stages of thrips and moved out during and after anthesis. After anthesis, the thrips that moved out of the corolla visited the flowers of the same branch/tree. These thrips were present only in day-1 and day-2 flowers despite the availability of full load or residual pollen and nectar in day-3 (Image 1j) and day-4 flowers. They collected pollen and nectar and carried pollen on their body as they were found coated all over with pollen; this foraging activity could affect pollination within and between flowers of the same tree but their role as resident foragers in the pollination is yet to be established. The fruit set rate was 21% in manipulated autogamy and 37% in geitonogamy.

G. latifolia flowers were not foraged by hawk moths during night time but were foraged by the Indian Flying Fox, *Pteropus medius* (Image 2a,b) as soon as the flowers were fully open by 1830 h and continued its foraging activity until 0300 h especially during peak flowering season (Table 1). This bat foraged for pollen only as there was no possibility for it to access the nectar which is deeply concealed and protected by a long narrow corolla tube. Since the stigma and dehisced anthers are placed at or slightly above the corolla throat, they easily facilitate the occurrence of pollination while the bat was collecting pollen. The bat always collected pollen from day-1 flowers only. The flowers visited by this bat can be easily identified by the marks of claws left on the corolla; the place of marks oxidize gradually and become prominent as brownish scars by the next morning (Image 1i). On the following day, the carpenter

bees, *Xylocopa pubescens* Spinola and *X. latipes* Drury (Image 2c) foraged for pollen collection from 0700 h to 1200 h with intense activity at 0900-1100 h (Table 1). These bees approached the flowers in upright position and probed from the flower-opening side to collect pollen which is situated at the corolla throat; the pollen collection activity results in the occurrence of pollination due to the placement of both stamens and stigma at the same place at or above the corolla throat. There is no possibility for these bees to collect deeply seated and concealed nectar with their short proboscis/tongue. They never made any attempts to rob nectar illegitimately bypassing the pollination apparatus and also never visited day-3 and day-4 flowers. Further, they never made any attempts to rob nectar illegitimately by making a slit into the corolla tube. The Purple Sunbird, *Nectarinia asiatica* Latham (Image 2d,e) and the Purple-rumped Sunbird *N. zeylonica* L. (Image 2f) foraged for nectar illegitimately from day-2 flowers from 0700 h to 1600 h due to a wide mismatch between the length of their beak and the length of the corolla tube to access nectar location (Table 1). They slit the mid-portion of the corolla tube from outside with their curved beak to access and collect nectar without effecting pollination. This illegitimate foraging behavior employed by sunbirds characterizes primary nectar robbing. These birds never made attempts to rob nectar from day-3 and day-4 flowers. Therefore, the pollination occurs in day-1 flowers by pollen collection activity of bats and in day-2 flowers by pollen collection activity of carpenter bees. Further, the sunbirds rob nectar only from day-2 flowers despite the availability of nectar in day-3 and day-4 flowers indicating that pollination occurs only in white-colored fragrance emitting from day-1 and day-2 flowers. Flower-handling time to collect pollen or nectar by each foraging species is given in Table 1.

G. latifolia flowers attracted a blister beetle, *Mylabris phalerata* Pallas (Coleoptera, Meloidae) (Image 2g). This beetle consumed the corolla, stamens and partially the stigma during the entire flowering season. Several individuals of this beetle were found on each flowering tree; 45% of the sampled flowers on each tree were found either damaged or completely consumed by it. This flower feeding activity by this beetle was found to be negatively affecting the reproductive success of the plant.

In the biotope of the same forest, the tree species, *Croton scabiosus* (Image 3a), *Cochlospermum religiosum* (Image 3c,d), and *Maerua apetala* bloom (Image 3e,f) simultaneously with *G. latifolia*. But, these tree species are not closely spaced and occur scattered at random.

Of these, *C. scabiosus* has considerable population while all other trees are represented by a few individuals. Of these, the first species is monoecious while the other tree species are hermaphroditic. Further, *C. religiosum* is nectarless while the other tree species are nectariferous. The carpenter bees used *C. religiosum* flowers as pollen source effecting pollination as in the case of *G. latifolia* while *M. apetala* (Image 3g) was used as nectar source effecting pollination. Since *C. religiosum* is represented by about ten individuals, there was no scope for competition between this tree species and *G. latifolia* for carpenter bees which collected only pollen from these species. Further, these bees used *G. latifolia* as pollen source only and *M. apetala* as nectar source, hence the question of competition between these species for pollination by carpenter bees was ruled out. Sunbirds, *N. asiatica* (Image 3b) and *N. zeylonica* used *C. scabiosus* as a source of insect food in the form of instars of larvae of an unidentified local butterfly; these birds picked up the larval instars from the leaves throughout the day. Further, these sunbirds also used *M. apetala* as nectar source by probing the flowers legitimately and effecting pollination (Image 3h,i).

DISCUSSION

Robbrecht (1988) reported that Rubiaceae members are entomophilous and the pollination mechanism in this family is conspicuously specialized via stylar modifications for passive pollen presentation. Anderson (1973) reported that in hermaphroditic isostylous flowers, protandry is predominant; the pollen matures early and is shed at or soon after anthesis. Before anthesis and in some cases for a period after anthesis, the elongation of the style is arrested, the immature stigmas are temporarily retained within the tube of the corolla, below the level of the anthers. During and/or after the release of the pollen the style elongates, eventually equaling or surpassing the anthers, and the stigmas belatedly mature. In this study, *G. latifolia* is a hermaphroditic isostylous species with weak protandry which occurs shortly before anthesis. The style elongation is not arrested but it continues to grow to surpass the dehisced anthers and matures as soon as anthesis occurs.

Puff et al. (2005) stated that protandry in isostylous flowers of Rubiaceae is associated with secondary pollen presentation. In this family, four types of secondary pollen presentation have been recognized according to the presenting area and receptive surfaces: i. pollen

deposition on the style only. Here, pollen deposition is strictly on non-receptive surfaces. The stigma and its receptive surfaces is higher up; 2. Pollen deposition on the style and outside of the stigma lobes. Pollen is solely deposited on non-receptive surfaces, but the abaxial surfaces of the stigma are also involved; 3. Pollen deposition on the outer side of the stigma; 4. Pollen deposition exclusively, largely or partly on the receptive surface of the stigma. In *G. latifolia*, the fourth type of pollen presentation mechanism is functional with partial pollen deposition on the receptive portion of the stigma. In this species, weak protandry facilitates overlap between the functional male and female stages within and between flowers of the same tree and hence, autonomous autogamy and geitonogamy are unavoidable (Bremer & Eriksson 2009) but the function of these pollination modes are not absolute. The secondary pollen presentation increases the efficiency and accuracy of pollen transfer because of the close proximity of pollen to the stigma (Ladd 1994). However, the proximity of pollen and stigma could also result in self-interference (Webb & Lloyd 1986), which is detrimental to plant fitness (Wailes & Agren 2006). In *G. latifolia*, autonomous autogamy and geitonogamy mediated by insects are advantageous since its flowering period falls in summer season when pollinating insects are mostly either unavailable or not reliable due to harsh ambient environmental conditions in the biotope of this species.

Consolaro et al. (2005) reported that species of Rubiaceae generally present a wide range of floral visitors. Puff et al. (2005) reported that Rubiaceae family members present a wide range of flower forms, sizes and colours indicating the involvement of many different pollinators and most of them are almost exclusively zoophilous. Most of these pollinators include insects while birds and bats play a minor role in pollination. Among insects also, bees are important pollinators especially for small-flowered species; the showy large-flowered species are adapted for pollination by butterflies and hawk moths. The butterflies are pollinators for scentless flowers while hawk moths for long-tubed fragrant flowers. Different authors documented that in dry lands of Africa, the Long-proboscid Hawk Moth *Agrius convolvuli* is an extremely abundant species comprising up to 50% of all hawk moths in local assemblages. Several hundred plant species have become adapted for pollination by this moth which is most likely a result of the abundance of its individuals (Martins & Johnson 2013; Johnson & Raguso 2016; Johnson et al. 2017). The biotope of *G. latifolia* is typically deciduous in nature with rocky

terrain and a few trees in bloom during the dry season. Despite the availability of fragrant flowers of this species and *Maerua apetala*, diurnal or nocturnal hawk moths never visited the flowers of these two species or any other species in the forest. Surprisingly, the bat, *Pteropus medius* consistently visits *G. latifolia* flowers for pollen collection although they are not appropriate for its visitation; its pollen feeding activity results in the occurrence of both self- and cross-pollination. The bat-visited flowers present brownish scars which can be taken as an indicator of bat foraging activity on this tree species. The *G. latifolia* flowers may produce tannins and the marks left by the visiting bats on corolla and stamens oxidize and appear conspicuous as brownish scars by the next morning. Jaeger (1961) reported that bats collect nectar and pollen from *Adansonia* flowers. He found considerable amount of pollen in the digestive tract of bats. Similarly, the bat visiting the flowers of *G. latifolia* collect pollen as a source of protein which would make an excellent balance in its diet with the sugar and water provided by nectar collected from other floral sources.

In *G. latifolia*, thrips by using the floral buds as breeding site and flowers as pollen and nectar sources as food could effect autogamy and/or geitonogamy but their role in pollination is yet to be studied. The carpenter bees, *Xylocopa pubescens* and *X. latipes* visit the flowers for pollen collection and in this act, they effect both self and cross-pollination but the flower is not appropriate for nectar collection by these bees as the flower is highly specialized with deeply seated nectar and a narrow corolla tube that prevents access to nectar by short-tongued bees such as carpenter bees. These bees also collect pollen from the simultaneously blooming *Cochlospermum religiosum* in the same forest. But, it is not known whether the same individuals of bees collect pollen from different floral sources alternately or exhibit fidelity to a particular floral source. Inouye (1983) reported that among insects, bees, wasps and ants are the most common primary nectar robbers of which bees make up the vast majority, and include carpenter bees, bumble bees, and stingless bees, and some solitary bees. They have some specific morphological structures to make holes on the corolla tube. Gerling et al. (1989) reported that carpenter bees use their maxillae to make slits in the sides of the flowers. Despite the copious amount of nectar produced by the flowers of *G. latifolia*, the carpenter bees never attempted to make a hole or slit in corolla tube tissue to steal nectar bypassing the floral opening used by legitimate pollinators although there is a dire need for nectar during the dry season. But, these bees collect nectar which is easily accessible by

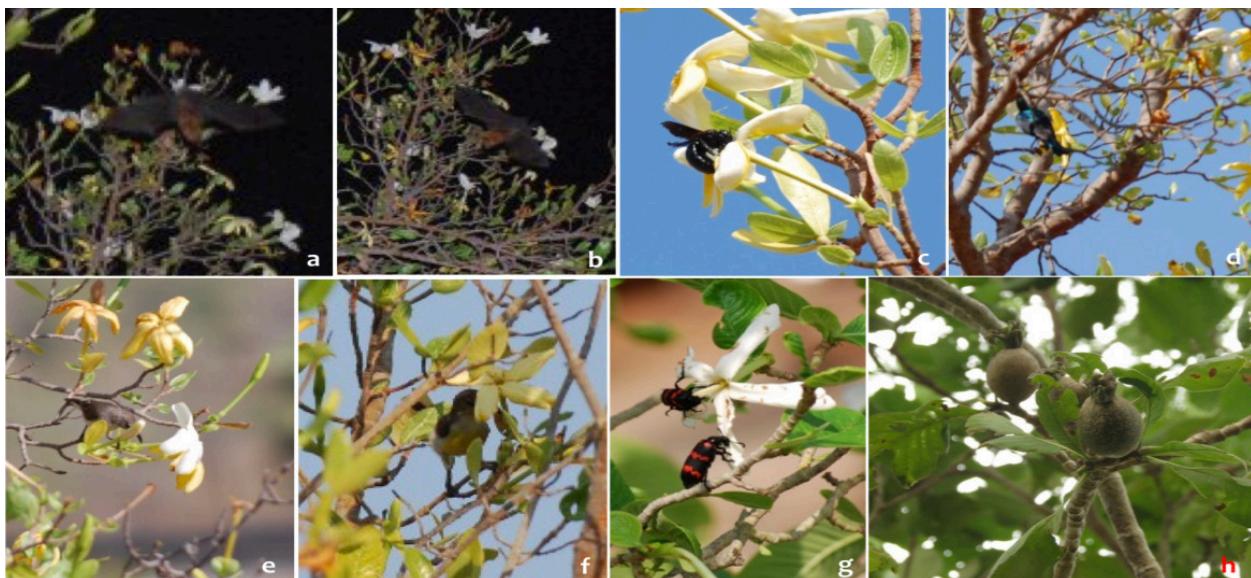


Image 2. *Gardenia latifolia*: a,b—Bat, *Pteropus medius* collecting pollen | c—*Xylocopa latipes* collecting pollen | d–f—Sunbirds robbing nectar by making a slit on the corolla tube from outside | d—*Nectarinia asiatica* (male) | e—*Nectarinia asiatica* (female) | f—*Nectarinia zeylonica* (female) | g—*Mylabris phalerata* feeding on flowers | h—Fruits. © Prof. A.J. Solomon Raju.

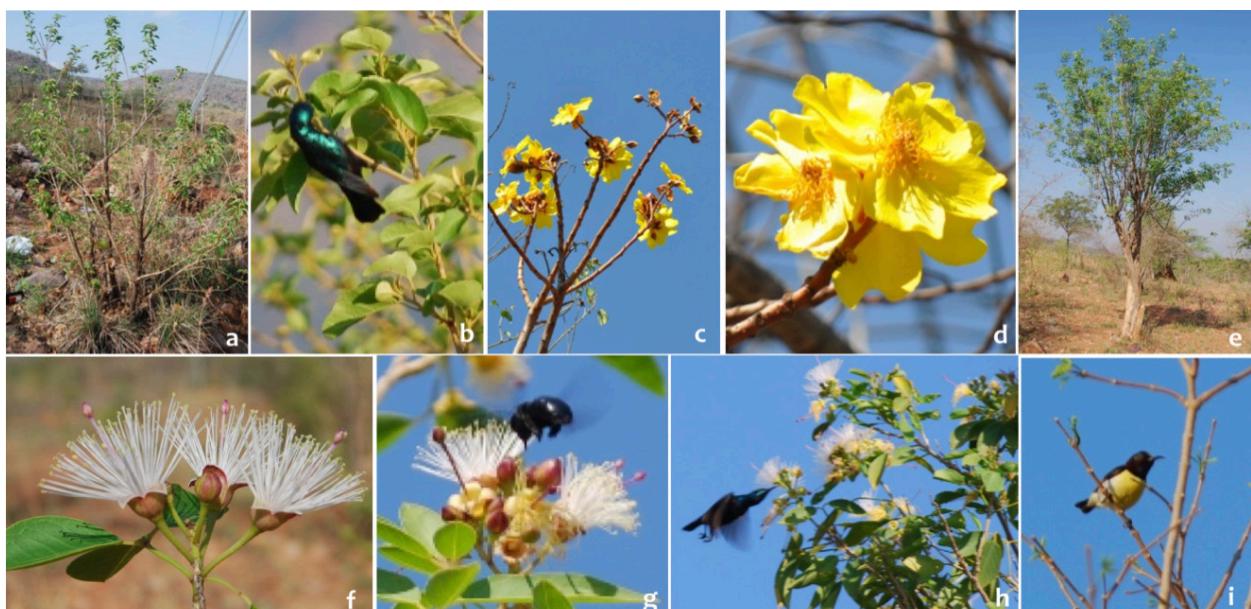


Image 3. Co-blooming tree species in the biotope of *Gardenia latifolia*: a—*Croton scabiosus* habit | b—*Croton scabiosus*—Purple Sunbird *Nectarinia asiatica* (male) collecting larval instars from the leaves | c,d—*Cochlospermum religiosum* | e–i—*Maerua apetala* | e—Tree habit | f—Flowers | g—Carpenter bee *Xylocopa latipes* collecting pollen | h—*Nectarinia asiatica* collecting nectar | i—*Nectarinia zeylonica* (male) perching. © Prof. A.J. Solomon Raju

legitimate probing from the flowers of *Maerua apetala* which blooms simultaneously in the same forest.

Castellanos et al. (2003, 2004) documented that floral adaptations that promote pollen transport by pollinators are treated as evidence of specialization to a particular pollinator type. Naravvo (2001) reported

that specialization in floral architecture is vulnerable to exploitation by flower visitors which remove or steal nectar without effecting pollination. Rojas-Nossa et al. (2016) stated that nectar robbers display a particular behaviour to steal nectar. A common form is primary nectar robbing in which the flower visitor makes a hole,

slit, or tear in corolla tissue to steal nectar bypassing the floral opening used by legitimate pollinators; this form of robbing is most common on flowers with hidden nectar. The flowers with tubular corolla are vulnerable to nectar robbing. Irwin & Maloof (2002) reported that another form of secondary nectar robbing in which the flower visitor acquires nectar through holes made by primary nectar robbers bypassing the floral opening used by legitimate pollinators. Irwin et al. (2010) reported that all flower visitors are not pollinators. Some visitors rob nectar bypassing the contact with the anthers and/or stigma and the effects of this nectar robbing behaviour by robbers range from negative to positive on female and male components of plant reproduction. Maloof & Inouye (2000) and Irwin et al. (2010) reported that nectar robbing is very frequent in plant species producing flowers with long corollas and abundant nectar production. In the present study, the sunbirds are just robbers of nectar of *G. latifolia* and this nectar robbing activity reduces nectar reward and increases variability in nectar standing crop. Such a situation is expected to promote pollination rate in general and cross-pollination in particular when legitimate pollinators visit *M. pubescens* flowers for nectar. Since there are no legitimate foragers to collect nectar from *G. latifolia* except the resident foragers, thrips, the nectar in this species remains in place if not utilized by sunbirds by robbing and hence the role of nectar in effecting pollination rate negatively or positively is totally ruled out. The absence of appropriate legitimate nectar seekers, diurnal hawk moths or nocturnal moths during the flowering season of *G. latifolia* could be attributed to unfavorable ambient temperature and unreliability of nectariferous floral resources with suitable nectar chemistry. Nevertheless, the availability of many flowering trees of *G. latifolia* during the dry season in this forest provides the needed levels of nectar for sunbirds that probe the flowers of this species illegitimately by robbing. It is interesting to note that bats use new and fresh flowers as soon as they are available upon anthesis and do not use the same flowers again on the next day or later while thrips use day-2 flowers also for forage collection. Bees and sunbirds use day-2 flowers only. All these foragers simply ignore day-3 and day-4 flowers which are faded by changing corolla color and lacking fragrance despite the availability of nectar in these flowers. This discriminatory behavior displayed by these foragers indicate that they use corolla color and strong fragrance as cues to visit the flowers of *G. latifolia*.

Puff et al. (2005) reported that fruits of Rubiaceae are of capsule type and classified into three types: those

that split open at maturity, those that break into one-seeded mericarps and those that remain indehiscent. The species possessing indehiscent fruits are either drupes or berry-like. Ornithochory is the most prevailing mode of seed dispersal. In *G. latifolia*, the fruit is an indehiscent berry with seeds enclosed by pulp inside. But, the pericarp is not very hard to break by birds with their bill, hence, it is most likely that birds are involved in seed dispersal when they feed on the pulp along with small seeds.

CONCLUSIONS

Gardenia latifolia is a semi-deciduous hermaphroditic dry season blooming tree species. The flowers are milky white and strongly fragrant on day 1 and day 2 while they are golden yellow and non-fragrant on days 3 and 4. They produce copious amounts of nectar which is concealed deep inside at the base of the narrow corolla tube. Thrips use the floral buds as breeding sites and flowers as pollen and nectar source. As resident foragers, they use day 1 and day 2 flowers only for forage collection. Bats visit only day 1 flowers for pollen collection while carpenter bees use only day 2 flowers for pollen collection. Like carpenter bees, sunbirds use only day 2 flowers for robbing nectar by probing the flowers illegitimately. The flower visiting activity of all these foragers indicates that they do not visit non-fragrant, golden yellow colored flowers although they possess nectar. Fruit is an indehiscent berry with seeds placed in pulp inside; the birds are the most likely seed dispersal agents when they break the pericarp and feed on the fruit pulp.

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