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POTENTIAL POLLINATORS OF UNDERSTORY POPULATIONS OF *SYMPHONIA GLOBULIFERA* IN THE NEOTROPICS

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Abstract—One difference between the forest canopy and the understory is that animals pollinate the majority of understory species in the tropical wet forest. Pollinators active in the understory are also different from those in the forest canopy and are adapted to the mesic conditions underneath the canopy. We used video cameras to observe flowers of understory *Symphonia globulifera* (Clusiaceae) in tropical wet forests of Costa Rica. We quantified the timing, frequency and behaviour of flower visitors to explore their potential contribution to pollination. A total of 82 flower visits were observed during 105 h of observations. Flowers were visited by ten insect species and one hummingbird species; the most active time period was between 1200-1700 h followed by the time between 0500-1000 h. The time period with fewer visitors was 1700-2200 h, during this period, we observed flowers being visited several times by a bushcricket (Tettigoniidae). The most frequent flower visitors were the stingless bee *Tetragonisca angustula* and the hummingbird *Phaethornis longirostris*; both came in contact with anther and stigma during visits. We observed different flower visitors from those reported for canopy populations of *S. globulifera.* Insects predominated, in contrast to observations in canopy populations of *S. globulifera,* where perching birds predominated. We also documented the consumption of pollen by visiting insects. These findings highlight differences in flower visitors between the forest canopy and the understory for the same tree species and contribute to better understanding of the pollination ecology of understory tropical wet forest species.

Keywords: Video observations, hummingbird, Neotropics, Orthoptera, Tetragonisca angustula, Phaethornis longirostris

INTRODUCTION

Tropical wet forests (TWF) are characterized by the immense diversity of taxa and complex vertical and horizontal structure. One characteristic that differentiates TWF from other forest biomes is that animals pollinate the great majority of tree species (Bawa et al. 1985; Dick et al. 2008). Differences among pollinators regarding behaviour and homes-range size create variation in the distance pollen is transported. In addition, the pollinator communities can differ between the several forest strata (Dick et al. 2008). Insects are the most important pollinator groups; vertebrates, such as birds and bats, also serve as pollinators, but for a smaller fraction of TWF species (3-11%) (Dick et al. 2008; Fleming et al. 2009). Among insects, bees constitute the most important group in number and diversity of plant species pollinated (Bawa 1990).

Pollinator-community surveys have traditionally been performed by direct observation and, more recently, by photography and continuous video recording (e.g. Bawa 1990; Quesada et al. 2003; Tschapka 2003; Lortie et al. 2012; Padyšáková et al. 2013). Identification of flower visitors and estimation of the frequency of visits are critical for evaluating animal pollination and obtaining an understanding of the plant-animal interactions that facilitate plant reproductive success (Bawa 1990; Vazquez et al. 2005). There are two key components of pollinator activity that determine pollinator performance: frequency and effectiveness of flower visits (Ne'eman et al. 2010). Visit frequency can be simply defined as the number of visits to a flower per unit of time. Effectiveness, also called efficiency, is open to various interpretations and it relates to the pollinator's behaviour during flower visits (visit duration, contact with reproductive structures), and the amount of pollen carried away and deposited on receptive stigmas (Sahli & Conner 2006; Ne'eman et al. 2009). Meta-analyses of plant-pollinator datasets indicate that the most frequent flower visitors generally account for >50% of the total pollination service (Vazquez et al. 2005; Sahli & Conner 2006). Visitation frequency has been suggested as an accurate surrogate of pollinators contribution to overall reproductive success (Vazquez et al. 2005; Sahli & Conner 2006; Ne'eman et al. 2009). However, existing data on plant-pollinator interactions have been derived from studies mostly of herbs and shrubs (Vazquez et al. 2005; Sahli & Conner 2006). Additional data are needed from animal-pollinated trees to achieve a more comprehensive understanding of the

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*Corresponding author: asanfiorenzo@gmail.com relationship between visitation frequency and pollinator importance.

In this study we identified the animals that visited flowers of *Symphonia globulifera* (Clusiaceae) in the Caribbean slope of Costa Rica. *Symphonia globulifera* has a broad distribution, being found throughout the Neotropics and in Africa. Perching birds and hummingbirds have been suggested to be the most important pollinators, at least in observations of populations in which adults reach the canopy (Degen et al. 2004; da Silva Carneiro et al. 2007; Dick & Heuertz 2008). We surveyed understory *S. globulifera* flowering trees in mature lowland TWF forest sites of Costa Rica, using video cameras to identify flower visitors. *Symphonia globulifera* occurs only as an understory tree in our study area, while in other regions it is a canopy tree (Degen et al. 2004; da Silva Carneiro et al. 2007; Dick & Heuertz 2008). Thus, we hypothesized that flower visitors of understory populations would be different from those of the canopy populations. We quantified the timing, frequency and behaviour of flower visitors. Visitation frequency and foraging behaviour are examined to explore the potential contribution to pollination by the observed flower visitors. We also discuss differences between the results of our study and those of studies of canopy populations of *S. globulifera*.

MATERIALS AND METHODS

Study area

We conducted this study in three mature forest patches in Sarapiquí County, Heredia Province, in the Caribbean lowlands of northern Costa Rica, centred at 10.440588 N, -84.115308 W. The study area is a 100 km^2 polygon that contains all three research sites (Fig. 1). This area is characterized by elevation that ranges from sea level to 300 m a.s.l.; terrain is a mixture of alluvial terraces, swamplands, and steep hills (Sesnie et al. 2008). Mean annual temperatures average 24°C and mean annual precipitation is 4000 mm per year (Sesnie et al. 2008). Land use is dominated by pasture, and recently pineapple cultivation has increased greatly. Other crops are also present intermixed with mature and secondary forest patches (Shaver et al. 2015).

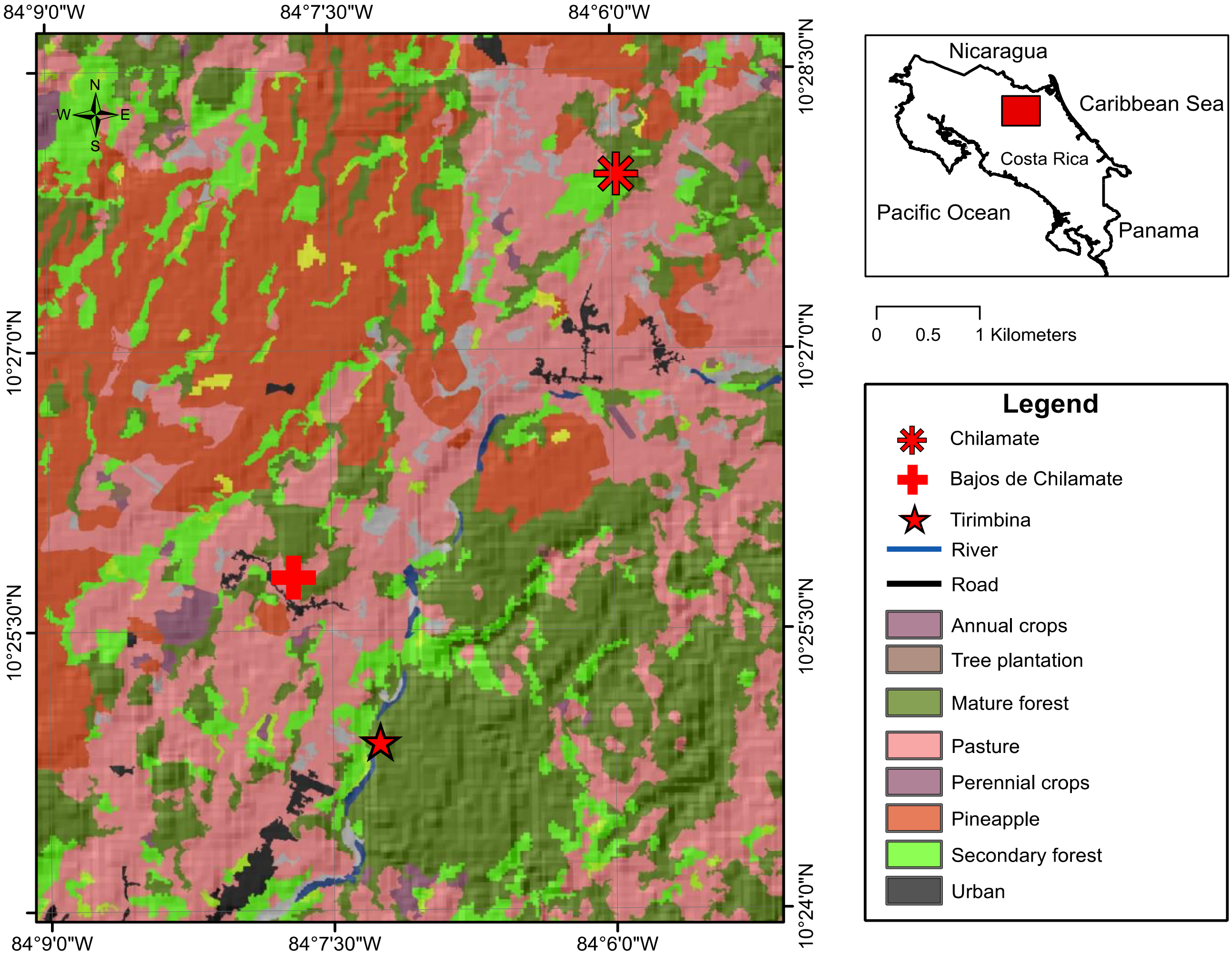

FIGURE 1. Study area, land cover and three sites where flower observations were performed. Land cover data source from Shaver et al. 2015.

Study species

Symphonia globulifera (Clusiaceae) is a shade-tolerant tree species distributed in rain forests across the Neotropics and equatorial Africa (Dick & Heuertz 2008). It is the only recognized species in its genus found outside of Madagascar, where 16 *Symphonia* species are present (Abdul-Salim 2002). Although *S. globulifera* are typically large canopy trees (Degen et al. 2004; Woodward 2005; Dick & Heuertz 2008), populations in the Sarapiquí region in Costa Rica occur only as understory trees, with a minimum reproductive size of 1 cm diameter at breast height (dbh, 1.3 m; personal observation). In French Guiana *S. globulifera* are large canopy trees that exist in two distinct sympatric forms, one with big leaves and the other with small leaves; they are treated as separate species by local forestry managers (Degen et al. 2004; Dick & Heuertz 2008). None of this morphological variation has yet been considered sufficient to merit splitting of *S. globulifera* into more than one Neotropical species (Dick et al. 2003; Dick & Heuertz 2008).

Inflorescences of *S. globulifera* consist of 1-15 axillary, bisexual flowers (Aldrich et al. 1998; Woodward 2005). Flowers are scarlet red, odourless, globose in shape, and more or less vertically oriented. At anthesis, petals contort and form a chamber in which nectar accumulates. Access to the interior chamber for flower visitors is only possible at the apex between the incurved petals and the staminal tube. The staminal tube surrounds the pistil; the anthers are inserted at the lobes of the staminal tube and open abaxially to display pollen immersed in a sticky, oily substance (Bittrich & Amaral 1996; Gill et al. 1998). A previous study found an unsaturated fatty acid methyl ester (methyl nervonate) to be the only component of the oil in which pollen is immersed. This secretion was thought to protect the pollen against foragers since no pollen foraging was observed (Bittrich et al. 2013). A well-developed nectary surrounds the base of the staminal tube. The stigma is shaped like a five-lobed star, with small pores at the apices of each lobe (Bittrich & Amaral 1996). Partial self-compatibility has been reported by Bittrich & Amaral (1996); however, the development of seeds through maturity was not followed, and the total number of viable seeds was not provided.

Pollination of *S. globulifera* flowers was described as mediated by sunbirds, wasps, bees, and butterflies in Africa (Oyen 2005). In French Guyana, perching birds have been described as potential pollinators (Gill et al. 1998). In Colombia, Brazil and Costa Rica, hummingbirds have been suggested as potential pollinators (Bittrich & Amaral 1996; Lasprilla & Sazima 2004). All the previous studies were carried out on canopy populations. Visits by euglossine (Apidae: Euglossini) and meliponine (Apidae: Meliponini) bees have been documented for the understory population in our study area (Rincón et al. 1999). Pascerralla (1992) conducted flower observations in the same area as the present study and reported hummingbirds as frequent flower visitors and nectar thieves, because no contact with fertile parts of flowers was observed. This author instead suggested Lepidoptera were probable pollinators, based on flower shape and plant distribution. *Symphonia globulifera* seeds are contained in large 4–5 cm drupes and are dispersed by bats and monkeys (Aldrich et al. 1998). The species is usually > 90% outcrossed (Degen et al. 2004; da Silva Carneiro et al. 2007), although some degree of self-fertilization (> 10%) has been documented in canopy populations in disturbed habitats in Costa Rica (Aldrich et al 1998).

Fieldwork

Trees were chosen based on the availability of flowers and accessibility, in three mature forest sites that offered security for the video recording equipment. In total, 25 flowers were observed, six flowers from one tree in Tirimbina, nine flowers from one tree in Chilamate and ten flowers from two trees (five each) in Bajos de Chilamate. Video recordings were performed during May and June 2013, using a Sony Digital Handycam HDR-SR10 with supplemented infrared light at night. The cameras were placed inside waterproof cases, sufficiently close (less than 3 m) to the flower to allow clear vision of the anthers and stigma. Video recordings were made during flower anthesis in three time periods: 0500-1000 h, 1200-1700 h and 1700-2200 h. In total, 105 hours of video recordings were analysed to assess flower visits, 35 hours from each time period.

Data Analysis

Video observations and analyses were performed using Adobe Premier software, through visual identification of the arrival of flower visitors. Animals observed were only considered visitors if they touched the stigmas or anthers or consumed nectar. Visits in which no fertile-part contacts were made or no nectar was consumed were not considered further. Most of these latter cases were by ants roaming around the flower petals. For each pollinator visit, the following data were recorded: duration of visit, whether stigma or anthers were contacted, and whether pollen or nectar was obtained. We considered pollen or nectar consumption if the buccal apparatus of the visitor touched the anther or accessed the nectar chamber and feeding behaviour was displayed (Sakamoto et al. 2012). Still images from the video were selected and used for identification. We calculated the visitation rate for each species, defining it as visits per flower per hour for each single recording period, then averaged across all observation periods.

RESULTS

A total of 82 visits to *S. globulifera* flowers were observed during the 105 hours of evaluated video recordings. The flowers were visited by ten insect species and one hummingbird species (Tab. 1, Fig. 2). We were unable to confidently identify two species, one small flying insect, probably a small hymenopteran or dipteran, and a nocturnal lepidopteran probably of the family Geometridae. These two visitors accounted for one observation each and were not considered in further analysis.

We observed four species of bees (Hymenoptera: Apidae): *Tetragonisca angustula* and three species of *Trigona*. Various ants (Formicidae) were observed: *Pseudomyrmex, Crematogaster* and *Solenopsis*. One wasp in the genus *Polybia* (Vespidae) was also present. Additionally, we recorded one species of hermit hummingbird *Phaethornis longirostris*

TABLE 1. Species visiting flowers of *S. globulifera*, including number of visits and frequency of visitation (*N* of visits per species/ total *N* of visits).

Class, Order	Family	Species	*N*	Frequency
Insecta,				
Hymenoptera	Apidae	*Trigona* sp. 1	2	0.03
		Trigona sp. 2	1	0.01
		Trigona sp. 3	5	0.03
		Tetragonisca angustula	25	0.29
	Formicidae	*Pseudomyrmex* sp. 1	1	0.01
		Crematogaster sp. 1	7	0.10
		Solenopsis sp. 1	17	0.25
	Vespidae	*Polybia* sp. 1	3	0.04
Orthoptera	Tettigoniidae	Tettigoniidae sp. 1	9	0.09
Aves,				
Apodiformes	Trochilidae	*Phaethornis longirostris*	12	0.13

(Trochilidae: Phaethornithinae) and one bushcricket (Tettigoniidae), Tettigoniidae sp.1.

Considering all observations together, the bee *Tetragonisca angustula* was the most frequent flower visitor, followed by the ant *Solenopsis* sp. 1, which was present on many occasions during diurnal observation periods. The hummingbird *Phaethornis longirostris* ranked third in visitation frequency with 12 observed visits. Other flower visitors were observed with lower visitation frequencies (Tab. 1). Visitation activities varied among time periods (Tab. 2). Visitors were more abundant during the 1200-1700 h time period with seven species recorded during this period. We observed *Pseudomyrmex* sp. 1, *Crematogaster* sp. 1*, Polybia* sp. 1 only during this period. In contrast, *Trigona* sp. 3, *Tetragonisca angustula, Solenopsis* sp. 1 and *Phaethornis longirostris*, were observed during two time periods (0500-1000 h; 1200-1700 h). The least active time period was between 1700-2200 h; the only visitor observed more than once during 1700-2200 h was the bushcricket (Tettigoniidae sp. 1), which was observed only during this observation period.

Visitation rate calculated as the average number of visits per hour reveals the number of interactions per unit of time. The highest visitation rate was for the bee *Tetragonisca angustula* with 0.28 visits flower^{-1} h^{-1}, followed by the ant *Solenopsis* sp. 1 with 0.21 visits flower^{-1} h^{-1} and the hummingbird *Phaethornis longirostris* with 0.13 visits flower^{-1} h^{-1} (Tab. 3). Other diurnal visitors showed lower visitation rates, some of which represent a single visit (Tab. 1, 3). During the 1700-2200 h time period Tettigoniidae accounted for 0.9 visits flower^{-1} h^{-1}.

Foraging behaviour during flower visits varied between species (Tab. 3). Eight species came in contact with the anthers during flower visits; only two ant species (*Pseudomyrmex* sp. 1 and *Crematogaster* sp. 1) did not touch the anthers while visiting flowers. Considering the species that touched the anthers, six were observed consuming pollen, that is, their buccal apparatus touched the anther area. We observed that seven species came in contact with the stigma while consuming pollen or nectar during flower visits. Seven species consumed nectar from flowers; the ants *Pseudomyrmex* and *Crematogaster* visited flowers to consume nectar and did not touch the anther or stigma. The hummingbird *P. longirostris* was the only species capable of accessing the internal chambers formed by the flower petals where nectar is accumulated; it used its long beak and tongue to consume the available nectar. During the short visits by *P. longirostris,* we witnessed direct contact between the upper beak and anthers and stigmas. We observed ants consuming nectar residues in the locations where *P. longirostris* had inserted its beak, immediately after the latter had visited. In general, visits by the ant *Solenopsis* sp.1 consisted of constant roaming around the flower, and we observed pollen and nectar consumption during flower visits. They moved over the anther multiple times during a visit; in some cases, individuals remained near or on the petals of the flower for the entire filming period. The other ant species, *Pseudomyrmex* sp. 1*,* and *Crematogaster* sp.1, were less frequent visitors, but showed a similar behaviour of roaming around the flower and consuming nectar.

The stingless bee *T. angustula* was the most frequent flower visitor, with a mean visit duration of 110 seconds. This bee spent most of the time eating and collecting pollen; most of its body touched the anther, and on many occasions the abdomen and legs contacted the stigma. Three species of *Trigona* bees also visited *S. globulifera* flowers; these visits were less frequent and their duration was shorter. One species of wasp, *Polybia* sp. 1, was also observed three times; it consumed pollen and roamed around the flower coming in contact with the stigma. Tettigoniidae sp. 1 was the only visitor during the 1700-2200 h observation period. It was observed after sunset touching the anther and stigma, this species accounts for the longest duration of visits with a mean value of 515 seconds. During its visits, Tettigoniidae sp. 1 spent most of the time consuming pollen and many parts of the upper body came in contact with anthers and on some occasions touched the stigma.

DISCUSSION

Nine insect species and one hummingbird were the most common and abundant flower visitors for *S. globulifera* in the understory populations of the Sarapiquí region in Heredia, Costa Rica. In the forest understory, insects and

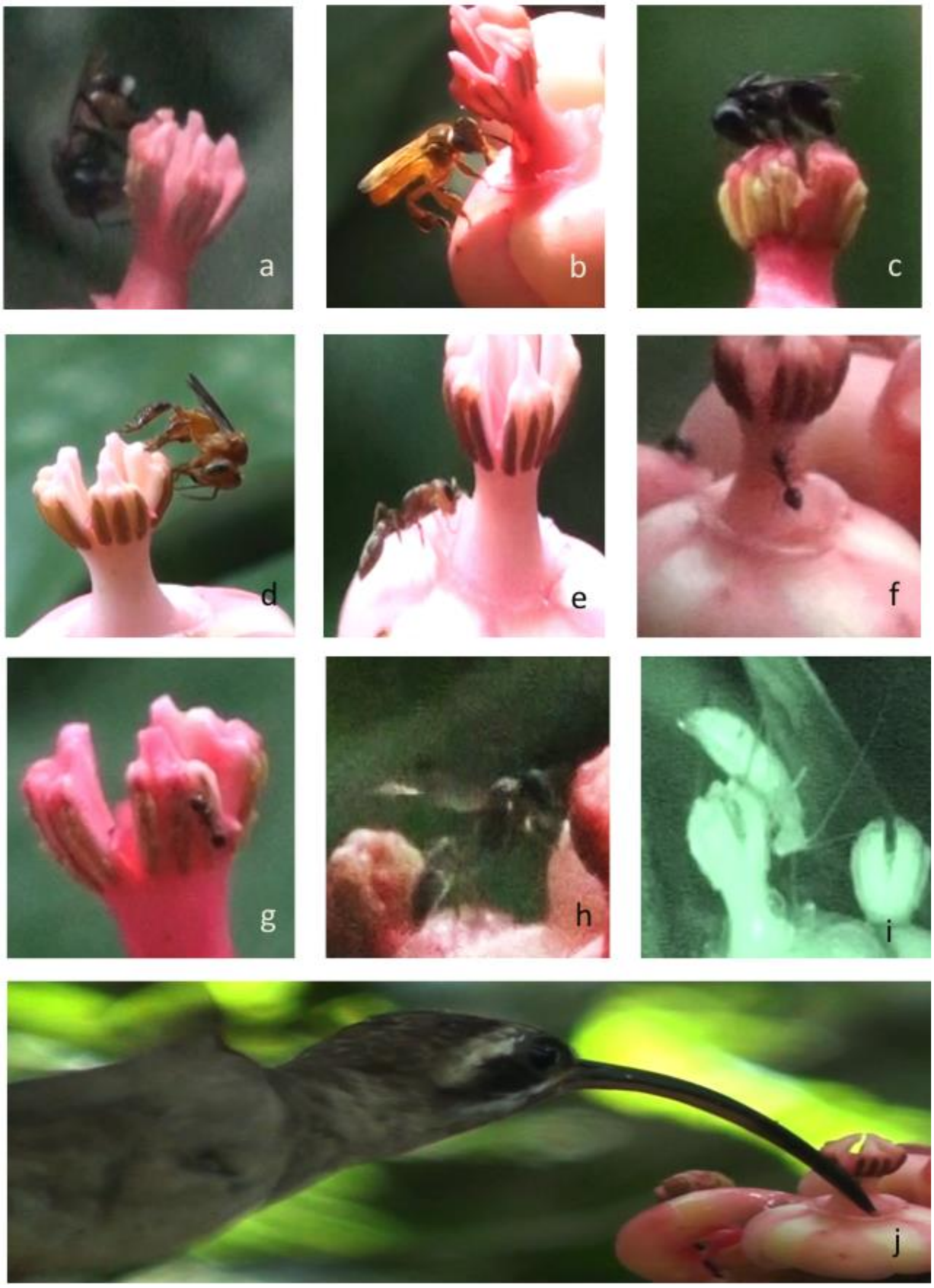

FIGURE 2. *Symphonia globulifera* flower visitors (a) *Trigona* sp. 1, (b) *Trigona* sp. 2, (c) *Trigona* sp. 3, (d) *Tetragonisca angustula*, (e) *Pseudomyrmex* sp. 1, (f) *Crematogaster* sp. 1, (g) *Solenopsis* sp. 1, (h) *Polybia* sp. 1, (i) Tettigoniidae sp. 1, (j) *Phaethornis longirostris*.

hummingbirds were the most frequent flower visitors of *S. globulifera*, in contrast to canopy populations of *S. globulifera* in French Guyana, where perching birds are reported as the main pollinators (Gill et al. 1998). Similarly, hummingbirds were suggested as the main potential pollinator in Brazil (Bittrich & Amaral 1996).

Flower visitors observed in this study are known to play important roles in the pollination of many plants in the TWF understory. Bees (Apidae) are often the most frequent visitors of flowers and the predominant pollinators for most plants and ecosystems (Neff & Simpson 1993; Winfree et al. 2011). Hummingbirds (Trochilidae) are found only in the Americas, and include 328 flower-visiting species (Winfree et al. 2011). In TWF hummingbirds are responsible for the pollination of herbaceous monocots in the genus *Heliconia* and also regularly visit flowers from a wide range of other species (Lasprilla & Sazima 2004). In some cases, hummingbirds have also been reported as nectar thieves and not true pollinators (Pascarella 1992; Muchhala et al. 2008; Hadley et al. 2014). Ants visiting flowers are usually considered non-pollinating insects (Hull & Beattie, 1988; Dutton & Frederickson 2012; Chacoff & Aschero 2014). However, there is evidence that ants can sometimes be pollinators since they are common flower visitors and are able to carry pollen that results in seed

TABLE 2. Number and frequency (*N* of visits per species in time period/ total *N* of visits in time period) of observed *S globulifera* flower visits by time period.

Species	0500-1000 h N	Frequency	1200-1700 h N	Frequency	1700-2200 h N	Frequency
Trigona sp. 1	2	0.07	0	0.00	0	0
Trigona sp. 2	1	0.03	0	0.00	0	0
Trigona sp. 3	1	0.03	4	0.09	0	0
Tetragonisca angustula	11	0.37	14	0.33	0	0
Pseudomyrmex sp. 1	0	0.00	1	0.02	0	0
Crematogaster sp. 1	0	0.00	7	0.16	0	0
Solenopsis sp. 1	10	0.33	7	0.16	0	0
Polybia sp. 1	0	0.00	3	0.07	0	0
Tettigoniidae sp. 1	0	0.00	0	0.00	9	1
Phaethornis longirostris	5	0.17	7	0.16	0	0
TOTAL	30		43		9	

TABLE 3. Foraging-behaviour data for visitors on *S. globulifera* flowers.

Species	Visitation rate (Number of visits/hour)	% of visits that				Visit duration (seconds)		
		contacted stigma	contacted anther	fed on nectar	fed on pollen	Mean	SD	Min-Max
Trigona sp. 1	0.02	100	100	0	50	11	1.4	10-12
Trigona sp. 2	0.01	0	100	0	0	5	0	5-5
Trigona sp. 3	0.06	80	80	20	80	11.5	13.4	2-21
Tetragonisca angustula	0.28	80	84	16	76	118.2	142.6	4-562
Pseudomyrmex sp. 1	0.01	0	0	100	0	181	0	181-181
Crematogaster sp. 1	0.06	0	0	100	0	74.57	95.5	16-289
Solenopsis sp. 1	0.21	71	88	29	76	143.65	105.1	18-453
Polybia sp. 1	0.03	100	100	0	67	18	11.5	7-30
Tettigoniidae sp. 1	0.09	78	100	33	100	515	545.3	115-1445
Phaethornis superciliosus	0.13	83	90	100	0	8.44	11	1-36

set (de Vega et al. 2009; Ashman & King 2005; Kawakita & Kato 2002). Neotropical tettigoniine bushcrickets are well known nocturnal florivores (Armbruster et al. 1997; Wardhaugh 2015) and are usually not considered to be pollinators (Schuster 1974; Proctor et al. 1996); their consumption of *S. globulifera* pollen in our observations suggests such a relationship here. However, Micheneau et al. (2010) reported that in wet lowlands forests the orchid *Angraecum cadetii* may be pollinated by leaf-rolling crickets (Orthoptera: Gryllacrididae). Furthermore, pollination by nocturnal visitors has been documented previously in the Clusiaceae; the cockroach *Amazonina platystylata* (Blattoidea: Blattidae) has been identified as the pollinator of *Clusia sellowiana* and *Clusia blattophila* in wet tropical forests of French Guyana (Vlasáková et al. 2008; Vlasáková 2015), although in these cases the insects feed primarily on special secretions instead of eating pollen. This raises the question as to whether the staminal secretions of *S. globulifera* might also play a role as reward for pollination services.

We observed that most insects came in contact with the anther and displayed pollen consumption behaviour during flower visits. For these flower visitors, it appears that the reward for visits was the pollen and oil solution present at the anther (Bittrich & Amaral 1996). This provides evidence of consumption for the unsaturated fatty acid methyl ester (methyl nervonate) in which pollen is immersed. This evidence was not available before, and absence of such observations led researchers to conclude that this substance provides protection against pollen foraging (Bittrich et al. 2013).

Many flower visitors made contact with the stigma and may therefore be potential pollinators. It is during this stigmatic contact that transfer of pollen, resulting in ovule fertilization, could occur. Visits from *Pseudomyrmex* and *Crematogaster* ants did not involve contact with the anther or stigma and probably reflect nectar foraging without any potential contribution to pollination. *Solenopsis* sp. 1 ants, one of the most frequent flower visitors, displayed similar behaviour, although they moved all over the flower, and we observed pollen consumption and brief contact with the stigmas. However, we observed that individuals from this species tended to stay in a single group of flowers for many hours, exhibiting opportunistic behaviour wherein ants seemed to be consuming nectar residues left on flower petals after hummingbird feeding. For these reasons we conclude that the potential of ants as pollinators for *S. globulifera* is minimal. The presence of ants did not seem to discourage other flower visitors, since in many occasions flower visits occurred with ants roaming on the petals.

Our results contrast markedly with studies of canopy populations of *S. globulifera.* In undisturbed lowland TWF of French Guyana, the most frequent and persistent flower visitors were five perching bird species of the family Thraupidae (Gill et al. 1998). Hummingbirds were also reported as regular flower visitors, but no insects were observed, and all flower visits were diurnal (Gill et al. 1998). In contrast, in Sarapiquí, a bushcricket (Tettigoniidae sp. 1) visited flowers during the 1700-2200 h period. In disturbed lowland TWF of Brazil, also for canopy populations, two species of trochiline hummingbirds (Trochilidae: Trochilinae) were the most frequent flower visitors (Bittrich & Amaral 1996). Insect visitors were also observed including *Trigona* bees. *Trigona* bees displayed destructive behaviour by chewing petals to access nectar, damaging or completely destroying the flowers; therefore, they acted as nectar thieves not pollinators for these populations (Bittrich & Amaral 1996).

We quantified interactions using visits per flower per hour; this metric allowed us to identify species with the most frequent interactions and therefore with greater potential for the pollination of *S. globulifera.*, assuming nearly equal efficiencies across pollinator species. Our results suggest that, considering foraging behaviour and visitation rates, the bee *T. angustula* and the hummingbird *P. longirostris* had the greatest potential contribution to the pollination of *S. globulifera*. Most flower visitors exhibited foraging behaviour that involved at least occasional contact with anther and stigma, also suggesting possible contributions to pollination. According to some research, the most frequent visitors usually contribute the most to the plant's reproductive success, even when their effectiveness is relatively low (Vazquez et al. 2005; Sahli & Conner 2006). However, flower visits do not necessarily indicate pollination; flower visitors are not always effective at both picking up and depositing pollen (Armbruster et al. 1989; Waser et al. 1996; Fenster et al. 2004; Ne'eman et al. 2010). Parameters such as visitation frequency, behaviour, morphology and effective pollen movement determine the pollination potential of flower visitors (Armbruster et al. 1989; Ne'eman et al. 2010).

Tetragonisca. angustula was the most frequent flower visitor. Behaviour during flower visits involved the consumption of pollen; in many instances their body parts came in contact with the stigmas of the flowers. This species had the highest visitation rate (0.28 visits flower^{-1} h^{-1}), more than twice that of the hummingbird (0.13 visits flower^{-1} h^{-1}). In this sense this is the flower visitor with the strongest interaction with *S. globulifera* flowers in this landscape. Not only is it a more frequent flower visitor than the hummingbird, the duration of visits is also longer, allowing for lengthier flower interaction time and contact with the flower stigmas. This stingless bee is distributed from Mexico to Argentina, one of the most widespread bee species in the Neotropics (Freitas et al. 2009; Camargo & Pedro 2013). They are generalists in their habits and have been identified as pollinators of many Neotropical plant species (Braga et al. 2012).

Hummingbirds were observed as frequent flower visitors of this understory tree population, which is consistent with observations in populations of canopy *S. globulifera* across the Neotropics (Bittrich & Amaral 1996; Gill et al. 1998; Lasprilla & Sazima 2004). The behaviour of *P. longirostris* during flower visits suggests they are potential pollinators because they contact anthers and stigmas while consuming nectar from flowers. The visitation rate for this species was 0.13 visits flower^{-1} h^{-1}. Visits were short (mean 8 seconds); however, we observed contact between the upper beak and the anther and stigma on more than 80% of visits. *Phaethornis longirostris* is a known *Heliconia* specialist (Snow & Texeira 2005). Evidence suggests this hummingbird species is tolerant of some degree of forest fragmentation (Hadley & Betts 2009; Volpe et al. 2014). Interestingly, *Phaethornis longirostris* is generally associated with understory habitats, not canopies, of mature and old secondary forests (Skutch & Dunning 1979; Johnsgard 1997).

The use of video cameras in this study allowed us to identify flower visitors and meticulously observe their behaviour during flower visits. The use of 16 frames-per-second and the high-definition video permit us to document flower visitors as ant's and bees. Our video recordings showed that hummingbirds do come in contact with flower reproductive parts and should not be considered as nectar thieves for this species. This differs from the direct visual observations of Pascarrela (1992), where no contacts with flower reproductive parts could be seen during hummingbird flower visits. This result may simply have been caused by the difficulty of visual observation of short hummingbird flower visits in the forest understory. Video records of flower visitors also provided evidence of pollen consumption not previously reported. Disadvantages are also associated with camera observation, such as the inability to observe visitor activities before and after the focal-flower visit, including movements among flowers and among trees. Future studies could address this by including human field observations or the use of more cameras, filming wider areas that cover the whole tree canopy. However, this would also increase the cost and logistic complexity associated with installing equipment in the field.

Conclusion

Previous studies of canopy populations of *Symphonia globulifera* described perching birds and hummingbirds as the most frequent flower visitors, with no insects reported as potential pollinators. We documented a different community of visitors to flowers of an understory population of *S. globulifera*. Twelve species, belonging to 5 families, were observed visiting flowers: 11 species of insects and one hummingbird. This suggests a shift in flower visitors between canopy and understory populations, emphasizing the difference between canopy and understory dynamics even for the same species. This difference in pollinators could generate a partial barrier to gene flow between canopy and understory populations, given that the most frequent pollinators observed in this study are associated with the forest understory rather than the forest canopy. Species observed visiting flowers in both canopy and understory populations are *Trigona* bees, suggested to be primarily nectar thieves in some instances. Nonetheless, these bees could be responsible for some pollen exchange between canopy and understory population. Further research in this area is needed to better understand gene flow between canopy and understory population of *S. globulifera*.

Based on visit frequency and rates of contact with fertile structures, the most important potential pollinators of *S. globulifera* understory populations were *T. angustula* and *P. longirostris*. Hummingbirds and bees, even if tolerant to forest fragmentation, require forest habitat to persist in the landscape (Brosi et al. 2008; Volpe et al. 2014). Thus, it is likely that forest fragmentation and subsequent land uses in the matrix can influence patterns of movement for these species and consequently the exchange of pollen for *S. globulifera* and other understory species throughout the landscape.

The present study increases our understanding of flower visitors and pollination in the tropical forest understory, specifically for *S. globulifera*. Further research on the deposition of pollen by each species can contribute to a more in-depth evaluation of individual pollinators' contributions to overall reproductive success. Effects of forest fragmentation should also be assessed in terms of loss of pollinators and reduction of *S. globulifera* populations in order to achieve a better understanding of the biological consequences of fragmentation in tropical wet forests.

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