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POLLINATION OF *NYPA FRUTICANS* (WURMB.) IN A SOUTH FLORIDA BOTANIC GARDEN

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Abstract—When plants are removed from their native habitat, reproduction can be compromised if pollinators are absent, especially when plant-pollinator interactions are species-specific and the plant is self-incompatible. To avoid these pitfalls, botanic gardens often use hand pollination to ensure reproductive success of their living collections, an important aspect of ex-situ conservation. The nipa palm, *Nypa fruticans*, presents an interesting case study of pollination in a botanic garden and a plant's ability to successfully reproduce outside its native range without assisted pollination. *Nypa fruticans* has been growing at Montgomery Botanical Center (MBC) in South Florida since 1984, but for years required hand pollination to produce viable fruit. A recent shift from hand pollination to unassisted pollination suggests that this palm has found an alternative to fertilize its flowers. We investigate possible pollinators and new opportunities for pollination outside the palm's native range. Rather than the insects typically associated with *N. fruticans* pollination in its native range in Southeast Asia (i.e., flies and beetles), ants, specifically *Paratrechina longicornis*, were overwhelmingly the most abundant visitors to nipa palm inflorescences at MBC and likely represent an important pollinator or facilitator of pollination at the garden. Pollination research at botanic gardens complements in-situ field studies and provides important insights into the flexibility of pollination systems to achieve reproductive success outside a plant's native range.

Keywords: Nypa fruticans, plant-animal interactions, nipa palm, ant pollination, mangrove, phenology

INTRODUCTION

Introduced exotic plants are not always able to reproduce outside their native range unless they are self-compatible or act as generalist species able to attract new pollinators from the local area (Thompson & Knight 2018). Plants that rely on specialized pollinators from their native habitat may be less integrated into exotic plant-pollinator networks, limiting successful reproduction outside their native range (Memmot & Waser 2002; Thompson & Knight 2018); however, if a plant is served well by generalist pollinators, then it will likely overcome these obstacles (Memmot & Waser 2002). The more generalized the pollinator, the more exotic plants it includes in its diet (Memmot & Waser 2002). Razanajatovo et al. (2015) suggest that plant species unable to maintain self-sustaining populations may be pollinator limited. Across Europe, invasive plants living among natives were frequently found to be visited by local native pollinators, and these pollinators often came to rely more on the invasive plants than the natives (Vilà et al. 2009). Sargent and Ackerly (2008) claim that plants in small, isolated populations have the most to gain from living among other plants that attract similar pollinators, dubbed pollinator facilitation. Under these circumstances, exotic plants can successfully establish within natural plant communities, although sometimes to the detriment of local plant species (Sunderland & Morakinyo 2002). Although the current literature on reproductive biology of exotic plant populations provides insights into pollinator limitation and facilitation of exotic and naturalized plant populations, information regarding pollination of exotic non-naturalized plants, such as those found at botanic gardens and arboreta, is scarce (Thompson & Knight 2018).

Successful fruit production by plants grown in botanic gardens and arboreta is never guaranteed, but oftentimes the mission of such gardens involves advancing ex-situ conservation through seed production. To overcome the absence of native pollinators, gardens sometimes rely on hand pollination to ensure successful reproduction, thus maintaining seed production for distribution and storage to conserve genetic resources for future generations. At Montgomery Botanical Center (MBC) in South Florida, garden staff hand pollinate multiple rare and endangered species, including several cycad species (i.e., *Cycas micronesica, Microcycas calocoma, Zamia lucayana*) and tree species, like *Brownea capitella* (Fabaceae). *Nypa fruticans* Wurmb. (Arecaceae), the mangrove palm commonly known as the nipa palm, is no exception. This species is native to Southeast Asia and grows mainly in brackish coastal areas. First planted at MBC in 1984, the garden's nipa palms represent the only known healthy collection of this species growing in North America. For years, successful fruit set

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required careful hand pollination, but in 2008 MBC scientists observed the first open-pollinated nipa fruits (Noblick et al. 2018). Shortly thereafter, a major freeze in 2010 destroyed all developing nipa inflorescences, but with time *N. fruticans* recovered. Hand pollinations resumed for a number of years, but the practice was discontinued in 2016. From 2017 onward, open-pollinated, viable nipa fruits have again been observed (Noblick et al. 2018). Has a mystery pollinator from South Florida assumed the role of pollinator in *N. fruticans*? Have the nipa palms at MBC resorted to self-pollination to successfully reproduce? In this study, we investigate the reproductive biology of *N. fruticans* grown in a botanic garden setting in South Florida, in order to identify the mysterious pollinator/s and discover how this palm species has been able to produce viable fruits without human intervention after several years of dependence on hand pollination.

MATERIALS AND METHODS

Study Site & Species Description

Montgomery Botanical Center (MBC; Coral Gables, Florida, USA) is a research garden in South Florida that focuses on palms, cycads, and tropical conifers. The climate is humid and subtropical, and over the past 20 years the area experienced an average annual temperature of 25.3ºC and average annual rainfall of 1698 mm (NOAA 2020), having wet summers and dry winters.

Nypa fruticans is one of only two palms known to live and grow with their trunk submerged underwater; the other being *Ravenea musicalis* from Madagascar. The nipa palm is native to estuarine mangrove vegetation and can be found in India and Sri Lanka, throughout Southeast Asia, and as far as Northern Australia. In the early 1900s, *N. fruticans* was introduced to Nigeria and has since spread and become invasive along the western coast of Africa (Numbere 2019; Moudingo et al. 2020). Additional reports of established populations in areas of the Caribbean, including Trinidad, Panama and Guyana, further attest to nipa's ability to thrive outside its native range (Noblick et al. 2018).

Nypa fruticans grows at four locations on MBC property, but thus far, successful fruit set has only been reported at two sites (Fig. 1). The garden palms were grown from seed collected in Malaysia and Indonesia in 1984 and 1998, respectively. The nipa palm has large pinnate leaves and a subterranean stem with dichotomous branching and is monoecious, displaying distinct male and female structures within the same inflorescence (Fig. 1B; Uhl 1972).

Nipa flowering is protogynous with the first male rachillae beginning to open a day after the onset of female anthesis (Mantiquilla et al. 2013). Multiple male spikes on each inflorescence open in succession over the next several days and produce large amounts of pollen. Nipa palms rely on insects for pollination (Essig 1973; Mantiquilla et al. 2016), as the spikey pollen grains are both sticky and heavy, making wind transport highly unlikely (Fig. 2). During receptivity, stigmatic fluid is present on the three separate carpels that make up each female flower and are arranged in a tight, single head (Fig. 1B). Fruits mature over several months into a large, heavy globular head (Fig. 1C), which may become so heavy in the wild that it topples into the water, where it breaks apart into individual floating fruits that disperse and establish themselves at new locations.

Nypa fruitcans phenology

Montgomery Botanical Center monthly phenology records from 1994–1997 were consulted to assess time of flowering. In addition, five inflorescences on two different plants were observed daily in 2018 for the duration of male and female anthesis, and photographic images were taken to characterize the flowering cycle from pre-anthesis through senescence. Each inflorescence was assigned a designated ID (i.e., A, B, C, D, E). Both the male and female parts are bright yellow orange when they emerge, and fade to a white or tan color, respectively, over time. To characterize the developmental stages of the inflorescence, we used color and woodiness for the female phase, and we visually accessed the amount of pollen for the male phase based on color and coverage of the anthers.

FIGURE 1. *Nypa fruticans* at Montgomery Botanical Center (MBC) in Coral Gables, Florida: (A) healthy stand of *N. fruticans* planted in 1984 and 1999, (B) recently opened *N. fruticans* inflorescence showing both the pistillate (female) flower head and newly opened staminate (male) flower spikes, and (C) developing *N. fruticans* infructescence head.

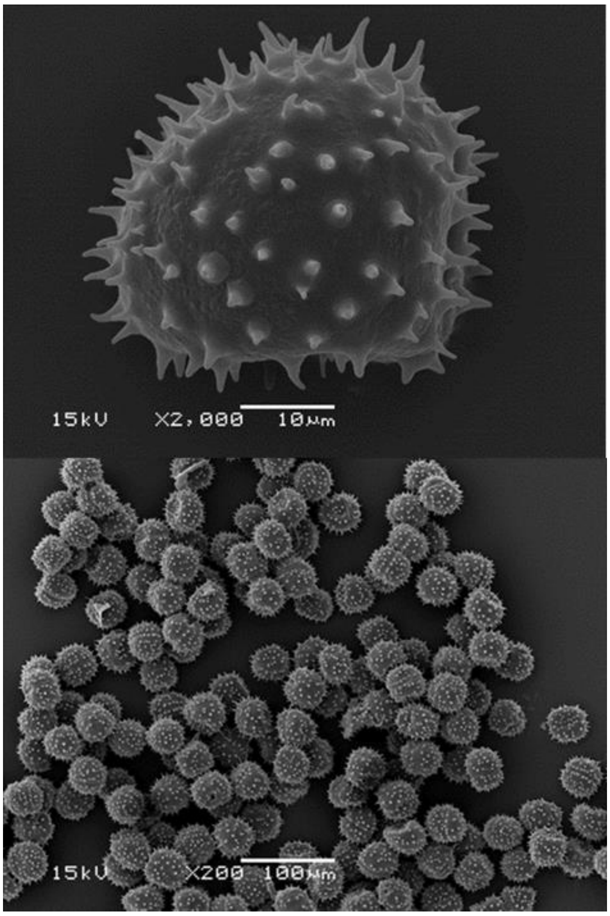

FIGURE 2. Scanning Electron Microscopic images of *Nypa fruticans* pollen collected at Montgomery Botanical Center in Coral Gables, Florida.

Pollinator Observations & Insect Collections

We determined insect visitors to *Nypa fruticans* through field observations and insect collections on the two nipa palms noted to have successfully reproduced without hand pollination. Between April and July 2018, we monitored five distinct inflorescences: A, B, C, D, and E. Both A and B underwent unstructured pollinator observations and collections. Inflorescences C and D followed a tight protocol to balance time between observations and collections, and inflorescence E was observed but no insect collections were carried out.

Due to a brief overlap in receptivity between the female and male anthesis within the same inflorescence (*ca.* one day), we alternated pollinator observations and insect collection times on sequential days for inflorescences C and D (e.g., Monday: morning observations, afternoon collections; Tuesday: morning collections, afternoon observations; Wednesday: morning observations, afternoon collections; etc.). Morning was defined as any consecutive two-hour period between 7:00 AM and 11:00 AM, while in the afternoon we recorded insects during a consecutive two-hour period between 12:00 PM and 4:00 PM.

For each observation, we recorded the date, start and end times, temperature (°C), and general weather conditions. We closely observed both the female and male flowers at a distance of approximately two feet from the center of the inflorescence. We documented insect visitors by functional group (i.e., fly, bee, beetle, ant, etc.) and noted any other identifying features. In all, we recorded approximately 47.75 hours of observations.

During collection times, insects that were seen interacting with the reproductive parts of the male and/or female flowers were collected using a vial aspirator with various 7.62 cm plastic tubes for storing the insects. During each collection, we divided insects into multiple plastic tubes for space and to avoid any negative interactions that could harm the sample. Overall, we spent 42.5 hours in the field collecting insects. Collected insects were identified by experts at Florida International University and the University of Florida/Florida Department of Agriculture and Consumer Services.

RESULTS

Flowering phenology

Monthly phenology records gathered at Montgomery Botanical Center between 1994 and 1997 indicate peak nipa flowering occurs during wetter summer months. We observed very few inflorescences during the dry/colder winter months in South Florida (January-March). Palms that were wild collected as seed from Malaysia began their flowering cycle two months before those from Indonesia.

At MBC, the female flower head emerges 1–2 days before any male flower spikes appear (Fig. 3). During these first days, the female flowers secrete clear stigmatic fluid, indicating receptivity (Straarup et al. 2018). By the fourth day after the pistillate head emerges, the stigmatic fluid begins to dry out, signaling the end of female receptivity and within eight days the flower head hardens into a woody mass of distinct carpels (Fig. 3). Approximately three days after the female flowers appear, multiple bracts containing male flower spikes open and more continue to emerge over the next several days. The male flower spikes show highest pollen loads during the first 2–3 days after emerging from their peduncular bracts, appearing bright yellow orange in color, and exuding a strong pungently sweet smell. Beginning on the third day, flower petals turn progressively beige, while the anthers and pollen fade to an off-white color (Fig. 3).

Insect Visitors

Four functional groups of insects were recorded during pollinator observations with ants being the most frequently observed (*N* = 156) (Fig. 4, Fig. 5). Flies were the second most often observed insect (*N* = 54), while bees (*N* = 7) and beetles (*N* = 2) were rarely seen (Fig. 4, Fig. 5). Insect collections corroborated our observations, revealing a greater presence of ants (*N* = 50) than any other functional group of insects. Otherwise, three flies, one planthopper (Fig. 4B), and one bee (Fig. 4C) were collected from the nipa inflorescences (Tab. 1).

The dominant visitor observed on female flowers was the ant: 91% of observed insect visitors (*N* = 51). The only other insects observed on the female flower head were flies (*N* = 6). Visitors observed on male rachillae were more diverse, with

FIGURE 3. *Nypa fruticans* inflorescence development through female (top row) and male (bottom row) anthesis, captured at Montgomery Botanical Center in Coral Gables, Florida.

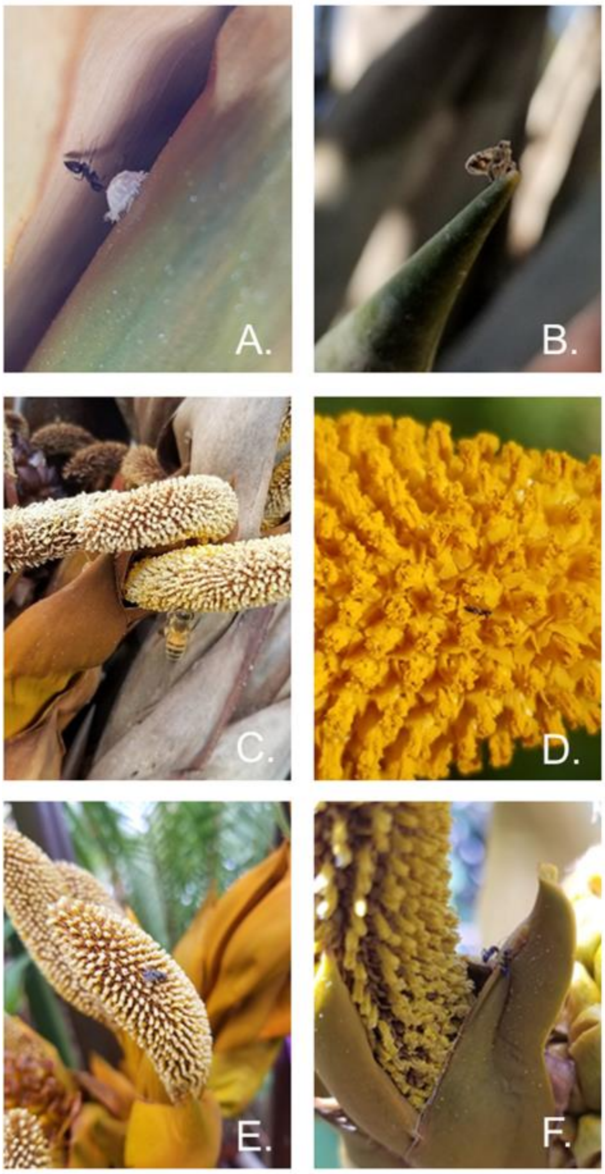

FIGURE 4. Insects observed on *Nypa fruticans* (A) *Paratrechina longicornis* tending a scale, (B) *Bothriocera* sp., (C) *Apis mellifera* on male, (D) unknown beetle on male, (E) unknown fly on male, and (F) two *Paratrechina longicornis* near male inflorescence.

the majority of visitors being flies (68%; $N = 40$), followed by ants (17%; $N = 10$), bees (12%; $N = 7$) and beetles (3%; $N = 2$). Only ants and flies were observed on both female and male flower structures. In addition to the ants observed on each sex individually, 30 more were observed crossing between male rachillae and female head, and we were able to track one fly as it travelled between female and male flowers.

We found no clear differences in insect visitation between AM and PM observations, although it should be noted that when combined, our data exhibited an unintentional skew toward morning observations and collections for all inflorescences except A. During observations and collections, temperature varied between 21–32ºC. Flower visitation rates showed no clear patterns associated with temperature—neither for insect visitors overall, nor for the distinct functional groups. We observed and collected the more common visitors (ants and flies) throughout the temperature range.

Ants & Nypa fruticans

Our pollinator observations and insect collections revealed an abundance of *Paratrechina longicornis*, commonly known as the crazy ant. They are common to the tropics and not generally recognized as pollinators (but see Takahashi et al. 1993). Crazy ants were seen walking between female and male inflorescences, sometimes carrying eggs, and at other times they appeared to be eating pollen or drinking the stigmatic fluid from receptive parts of the female flowers. We observed clumps of pollen grains on the exterior of the ants' bodies, clearly visible to the naked eye and could see ant mandibles moving but could not confirm that they were consuming pollen.

DISCUSSION

Pollination and successful fruit set of non-native plant species conserved in botanic gardens and arboreta present intriguing questions that remain poorly understood. In ex-situ conservation, curators often rely on hand pollination to ensure purity of offspring and help guard against the reproductive failure in non-anemophilous species growing outside their native range. Within the context of botanic gardens, many conspecifics with distinct native ranges thrive together in one place, and pollen limitation often compromises successful

TABLE 1. Total counts of observed and collected insect visitors to *Nypa fruticans* growing at Montgomery Botanical Center in Coral Gables, Florida.

Insect Functional Group	Total Insects Observed	Total Insects Collected	Species name*	Order	Family
ant	156	50	*Paratrechina longicornis* (Latreille)	Hymenoptera	Formicidae
fly	54	4	*Drosophila* sp., subgenus *Sophophora* and Unknown	Diptera	Drosophilidae and unknown
bee	7	1	*Apis mellifera* Linnaeus	Hymenoptera	Apidae
beetle	2	0	*Typhaea stercorea* (Linnaeus) and Anthocoridae	Coleoptera	Mycetophagidae and Anthocoridae
planthopper	0	1	*Bothriocera* sp.	Hemiptera	Cixiidae

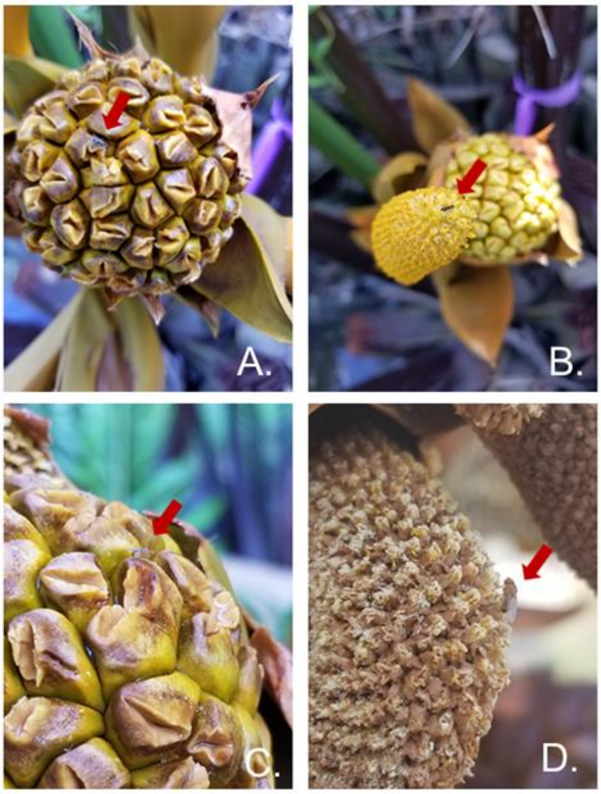

FIGURE 5. Female (L) and male (R) inflorescences of *Nypa fruticans* with (A, B) *Paratrechina longicornis* and (C, D) *Drosophila* sp.

fruit production. For this reason, successful *N. fruticans* fruit set after hand pollination stopped at MBC is particularly interesting. Not only are the palms growing outside of their native range, far from native pollinators, they have no conspecifics with which to hybridize. This species has either been exposed to local insects that fill the role of pollinator, or self-fertilization has found success in these palms after a period of adaptation. The oldest nipa palms at MBC, planted in 1984, have been flowering for the past 25 years. A recent uptick in inflorescence production as younger specimens, planted in 1999 and 2000, matured may have triggered elevated pollen availability–enough for local pollinators to show an interest in this species, thus surmounting issues of pollen limitation (Burd 1994). Alternatively, autogamy is theoretically possible due to the brief overlap in male and female anthesis within the same inflorescence. Similar to our findings, Mantiquilla et al. (2018) reported that stigma receptivity peaks at 12 h after anthesis and significantly declines after 48 h completing the cycle within 72 h. At MBC, male flower spikes begin opening the second and third day after the female flower head emerges, making self-fertilization theoretically possible.

The possibility of wind pollination is unlikely. Nipa pollen is sticky and heavy (Essig 1973). Furthermore, the position of the male rachillae, generally to the sides and beneath the female flower head, reduces the chance that pollen will fall onto receptive female flowers. These characteristics suggest *N. fruticans* is not adapted for anemophily as a primary mode of pollen transfer, but rather point to entomophily as the principal means to reproduction. Studies from its native range in Southeast Asia highlight beetles, weevils, flies, and bees as potential pollinators of *N. fruticans* (Essig 1973; Tan 2008; Mantiquilla et al. 2016; Panabang et al. 2017; Straarup et al. 2018). To our surprise, these native pollinator groups were extremely rare on nipa inflorescences in the garden. Ant visitors greatly outnumbered beetles, flies, and bees observed on nipa inflorescences at MBC.

A key detail in confirming an insect's role as pollinator is activity on both male and female flowers. Without this overlap, insect visitors are largely inconsequential. We frequently witnessed ants traveling between male and female flowers. Flies also visited both male and female inflorescences, although they preferred male flowers. Only a single fly was observed flying between male and female flower branches, but the difficulty of following flying insects after they take flight may explain this low rate of observation. Since bees and beetles were only observed or collected on male flowers, we assume they play no significant role in nipa pollination at MBC.

While ants were clearly the most abundant visitors to the nipa flowers at MBC, until recently their role as pollinator has been downplayed in the scientific literature. Ants produce an antimicrobial secretion that can reduce pollen viability (Beattie et al. 1985), and this negative role in pollination has been widely assumed to be the norm until recently, as a growing number of studies have demonstrated effective pollination by ant species in some plants (Hickman 1974; Rostás & Tautz 2011; De Vega & Gomez 2014; Domingos-Melo et al. 2017; Delnevo et al. 2020). The ant species found on our nipa palms, *Paratrechina longicornis*, is widespread in the U.S. and does not appear to be a newcomer to South Florida. Other nipa studies reported the presence of ants but discarded them as potential pollinators. In Thailand, Hoppe (2005) observed ants on nipa flowers during anthesis but assumed they play only a minor role in self-pollination. In the Philippines, Panabang et al. (2017) observed ants on nipa pistillate heads, feeding on gelatinous stigmatic secretions, but attributed their presence to aphids that serve as a source of honeydew. At MBC, we also observed ants tending to aphids on nipa inflorescences (Fig. 4A). In Thailand, Straarup et al. (2018) regularly observed "patrolling ants" on nipa inflorescences, presumably collecting stigmatic fluid from female flowers, but unlike our study, these same ants rarely visited male rachillae during female anthesis. If ants are indeed the nipa pollinator we are looking for at MBC, our study represents one of the rare cases where an ant acts as pollinator, and the first reported instance of ant pollination in a species outside its native range. Since travel between different inflorescences is highly unlikely with nipa inflorescences often blooming at least several meters apart, the ants' role may be restricted to facilitating self-pollination rather than effecting cross-pollination. If nipa palms are relying on ants for pollination, and consequently self-pollination dominates, then inbreeding depression might help explain the low success rate of fully developed fruits per female inflorescence head that we observed at MBC (*cf.* Rostás et al. 2018).

In *Nypa fruticans*, stigmatic fluid on the receptive carpels of the female flower head attracts insects (Hoppe 2005), along with a distinct floral scent, which is intensified by the heat of thermogenesis. The floral scent chemistry for *N. fruticans* contains compounds that are highly attractive for Scarab beetles (Scarabaeidae) and some flies (Azuma et al. 2002). Flies were the second most common visitor to nipa at MBC, yet their abundance paled in comparison to the number of ants recorded. Within nipa's native range, flies are repeatedly cited as potential pollinators (Essig 1973, Mantiquilla et al. 2016, Panabang et al. 2017). Diptera were the most abundant insects (48%) in Philippines' nipa stands, followed by Coleoptera (beetles; 22%) (Panabang et al. 2017). Panabang et al. (2017) observed *Musca* sp. flies laying eggs on nipa inflorescence bracts and *Drosophila* spp. feeding on pollen and stigmatic fluid. Essig (1973) observed drosophilid flies on both male and female nipa flowers in Papua New Guinea and found that nipa inflorescences provide a burrowing-feeding site for fly larvae, and when adult flies emerge, their pollen-covered bodies carry pollen to other inflorescences. Mantiquilla et al. (2016), also identified both drosophilid flies and nitidulid beetles as likely pollinators of nipa flowers in the Philippines. Panabang et al. (2017) and Straarup et al. (2018) agree that nitidulids (sap beetles) and curculionids (weevils) play a key role in *N. fruticans* pollination across their native range. During thermogenesis, the female nipa head warms up to six degrees Celsius above ambient temperature before opening (Straarup et al. 2018). This attracts insects, particularly ovipositing beetles, as warmth promotes egg and larvae development (Barfod et al. 2011). The inflorescence also serves as an ideal breeding and brood site for insects due to the many layers of bracts that envelop its inflorescence structures (Panabang et al. 2017). Weevils were mostly found inside inflorescence bracts, but they also visited flowers of both sexes. Panabang et al. (2017) also observed pollen-covered sap beetles visiting the pistillate head of nipa inflorescences and noted that smaller sap beetle species and weevils have an advantage in pollination as they are small enough to crawl into the locular canals of the female flower head, facilitating pollination. At MBC, we collected neither sap beetles, nor weevils. Instead, we encountered beetle species from the Mycetophagidae and Anthocoridae families. This was somewhat surprising, since Nitidulidae and Curculionidae are widely distributed throughout South Florida (Parsons 1943; Giblin-Davis et al. 1996).

In spite of nipa's dependence on insect pollinators in their native range, self-compatibility cannot be excluded (Straarup et al. 2018). Hoppe (2005) found no fruit set in three inflorescences bagged as part of his pollinator exclusion experiment. Mantiquilla et al. (2016), on the other hand, reported 50% fruiting success from self-pollination in Philippine nipa populations, but with a caveat: loosely tied pollinator exclusion bags may have unintentionally permitted the entrance of pollinators. Preliminary results at MBC indicate successful self-pollination in at least two of three inflorescences bagged for pollinator exclusion (unpublished data) and raises the question as to whether mature fruits found at the garden resulted from self-pollination. Even so, this fails to explain why successful fruit set has only occurred within the last decade. A likely explanation is an increase in flowering frequencies and pollen availability as our *N. fruticans* collections have matured, coupled with the introduction of a new pollinator to the area, or heightened interest from local pollinators that have either facilitated self-pollination or played an active role in cross-pollination. Overall, fruit set remains low but persistent for open pollinated *N. fruticans* at MBC. Nipa palms at MBC produce more failed infructescences (with aborted fruit) than mature infructescences, and even the successful infructescences usually bear only a handful of viable fruits per head. This suggests reduced success rates due to selfing (Mantiquilla et al. 2013), or pollen limitation. Molecular analyses of our nipa palms and their offspring would help clarify these unknowns. Whether it is self- or cross-pollination, one thing is certain: open pollinated nipa flowers are now producing viable seed.

Due to their large numbers and visitation to both male and female flowers, ants are likely to be contributing to pollination of *N. fruticans* at MBC. Inflorescence architecture and the timing of the male and female phases strongly favors cross-pollination by minimizing chances for self-pollination, but pollinators with a restricted foraging range, such as ants, could be facilitating self-pollination (Peakall & Beattie 1991; Gomez & Zamora 1992; De Vega et al. 2009), albeit at a low success rate. Pollination research in botanic gardens complements field studies and provides insight into flexibility of reproduction outside of a species' native range, producing valuable information for ex-situ conservation efforts.

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