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Research Article

Are Native Palms "Pollinator Hogs"? A Field Experiment in Pine Rocklands of Southern Florida

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ABSTRACT

Plants blooming simultaneously may interfere with each other's pollination (competition for pollinators) or enhance each other's pollination (pollinator sharing). In this study we asked the question: What is the effect of native palm flowering on the pollination of a native wildflower species? Using potted plants of pineland golden trumpet *Angadenia berteroi* (Apocynaceae), we placed plants with flowers about to open in the field in two positions: within 5 m of flowering palms (*Sabal palmetto* and *Serenoa repens*, Arecaceae), and within 5 m of palms that were not flowering. We observed visitors to the flowers of *A. berteroi* on plants in both situations. We collected the corollas of the one-day flowers to look for pollen deposition on the receptive stigmatic surface. The same flowers were monitored to see if they set fruit. Flowers on plants in both situations were visited, but the ones near flowering palms less frequently. More of the flowers from plants near non-flowering palms had pollen deposited on the stigma, but fruit from flowers presented did not differ between treatments. This experiment demonstrates that flowering palms, with their large floral displays full of pollen and nectar, diminished pollinator visits to one of the most beautiful of the pine rockland wildflowers, resulting in less pollination in *A. berteroi*. As fire suppression can lead to an understory with overrepresentation of understory palms in pine rocklands, practitioners should manage natural areas to prevent these super-attractive species from hogging floral visitors to the detriment of less numerous native wildflowers.

Index terms: flowers; pine rocklands; pollination; wildflowers

INTRODUCTION

Plants that bloom at the same time may interfere with each other's pollination in competition for pollinators. Alternatively, they may enhance each other's pollination via pollinator sharing. Over the last several decades, many studies have examined pollination interactions between co-blooming plants, with different findings. When pollination of one species is diminished in the presence of another, competition for pollinators is indicated (Waser 1983). This may take place between/among native plant species (Waser 1978a, 1978b; Campbell 1985; Campbell and Motten 1985; Waser and Fugate 1986; Galen and Gregory 1989; Ha and Ivey 2017), as well as in nonnatives competing with natives (McKinney and Goodell 2010, 2011; DaSilva and Sargent 2011; Dietsch et al. 2011; King and Sargent 2012; Thijs et al. 2012; Molano-Flores 2014; Bruckman and Campbell 2016) for pollinators. When a species receives more pollen when blooming alongside another, there is evidence of benefit from pollinator sharing (Schemske 1981; Feinsinger et al. 1986; Duffy and Stout 2011). This may also occur between invasive and native species (Masters and Emery 2015; Montero-Castaño and Vila 2015; Muir and Vamosi 2015; Groulx and Sargent 2018), and even invasive species with other invasives (Molina-Montenegro et al. 2008).

Some plants are good at attracting floral visitors and rewarding those visitors; their presence may therefore benefit other plants. Such plants were dubbed "magnet species" (Thomson 1978), whereby species that depend on pollinator visits, but are less attractive or do not offer floral rewards, may have greater floral visitation and enhanced reproductive success (pollen receipt and fruit set) near "magnet" species. In Thomson's study, he observed two hawkweed species; *Hieracium aurantiacum* (orange flowered) was much more attractive to visitors than was *H. florentinum* (yellow flowered). As the yellow-flowered plants got more visits when there were more orange ones around them, the conclusion was that orange hawkweeds are "pollinator magnets." The magnet effect exists between lousewort and mayapple: their proximity to lousewort (which produces lots of nectar, and is very popular with bumblebees) enhanced mayapple fruit and seed set (Laverty and Plowright 1988; Laverty 1992). In Swedish meadows, non-rewarding orchids received many more visits from bumblebee pollinators when the orchids were in patches with nectar plants than when they were without them (Johnson et al. 2003).

The proximity of a very attractive species (a so-called magnet species) can be a good thing, as nearby plants may benefit from its presence; in some situations, however, these super-attractive plants may monopolize the visitors, in a situation that we suggest be called "hogging" the pollinators. More than an alternative interpretation of the pollinator magnet situation, this is an example of extreme competition, where the presence of one may eclipse the flowers of the less obvious plants blooming nearby.

An extreme case of competition for pollinators may occur when there are species so numerous, and abundantly rewarding, that they eclipse all other flowers in the vicinity. Flowers of other species, even if they also provide rewards, may get little or no visitation if they are too close to the super-attractors, and blooming near such a "hog" may be detrimental to a plant's pollination. Seifan et al. (2014) placed potted individuals of attractive *Centaurea cyanus* (cornflower) in high- and low-density arrays in meadows, and measured effects on other attractive and less attractive species. The cornflower attracted visitors that benefited the other plants in low density but was a successful competitor for visits when present in high density. Their experiments showed that the density of the attractive flowers made a difference in pollination of less attractive flowers.

In natural areas of southern Florida, a single flowering palm inflorescence provides hundreds of nectar-producing flowers at high densities. While watching for floral visitors to various low-growing perennials in natural areas, we noticed that flowers of our study species were not visited during some observation periods (Pinto-Torres and Koptur 2009; Cardel and Koptur 2010; Linares and Koptur 2010; Barrios et al. 2016; Koptur and Khorsand 2018). However, in those same studies, a variety of insects visited the large inflorescences of native palms nearby. For this reason, we sought to determine whether flowering palms act as pollinator hogs, or pollinator magnets, asking the question: How does proximity to an attractive species with abundant flowers (palms) affect visitation to nearby wildflowers? If the palms hog the floral visitors, it will be an extreme case of competition for pollinators with co-blooming wildflowers; if they draw in so many visitors that the wildflowers also benefit, acting as a magnet, it will be a case of facilitation, or pollinator sharing. To answer this question, we used an experimental approach, putting out potted plants of an understory plant routinely visited by bees and butterflies, and measuring flower visitation, pollen deposition, and fruit set when they were near or far from a native flowering palm.

METHODS

Study Species

Target Species: The pineland golden trumpet (Figure 1), *Angadenia berteroi* (A.DC.) Miers (Apocynaceae), is state listed as threatened in southern Florida, and was considered one of the species of positive interest in vegetation surveys conducted in Miami pine rocklands (Possley et al. 2008). Its abundance, flowering, and fruiting are associated with open pine rockland understory, with minimal leaf litter and relatively recent fire (Barrios et al. 2011; Barrios et al. 2016). In the northern part of its range (the Biscayne region) it was most prevalent in unburned areas, but in the southern part of its range, the Redland region, its greatest coverage was in plots that experienced multiple burns (Possley et al. 2014). A low-growing herbaceous perennial, *A. berteroi* has narrow leaves on slender stems bearing showy yellow flowers (Barrios and Koptur 2011). Flowers open in the early morning and last a single day, often falling off by late afternoon the same day. The stigmatic surface remains attached to the fallen corolla, allowing estimation of pollen deposition in that flower. Few flowers set fruit, and hand-pollination experiments showed *A. berteroi* is self-incompatible, and pollinator-dependent for sexual reproduction (Barrios and Koptur 2011). Visitors to its flowers may get pollen attached to their mouthparts via mucilage applied by the flower's style head and include long-tongued and short-tongued bees (Figure 1), butterflies, and skippers (Figure 2). It appears that larger bees are its most effective pollinators, as a single visit can result in fruit production (Barrios et al. 2016). The peak flowering time for this species in the field is April and early May. Our experiment took place from mid-May to early June, when *A. berteroi* flowers were very few on naturally occurring plants in the field, but still numerous on the potted plants cared for in the greenhouse that we transported to the field for experimental placements.

Palm Species: Pine rocklands of southern Florida have several native palm species (Arecaceae) in the understory (Koptur and Khorsand 2018), the two most common being *Sabal palmetto* (Walt.) Lodd. ex J.A. & J.H. Schultes and *Serenoa repens* (W.Bartram) Small. Though easily distinguished vegetatively, they both have many small white flowers produced in large inflorescences that open over many days. The flowers of the large inflorescences produce nectar, have a sweet, pleasant smell, and visitors are usually numerous. These two palms share many floral visitors in south Florida pine rocklands: honeybees, native bees, wasps, moths, and butterflies (Koptur and Khorsand 2018). They also share visitors with *Angadenia berteroi* (Barrios et al. 2016), particularly bees and butterflies. Both palms may be found in flower any month of the year, and many have inflorescences in spring and early summer, at the time of this study. Silver palm (*Coccothrinax argentata*) is also found at our study site, but was not included as one of the "flowering palms" used in this study, as it is less frequent, not many were blooming at the time, and its flowers offer only pollen as a floral reward, while the other two palms have nectar as well as pollen (Khorsand Rosa and Koptur 2009).

Study Site

Pine rockland is a critically imperiled, globally (G1) imperiled habitat in southern Florida, with a very small percentage of its original extent along the Miami Rock Ridge preserved in protected natural areas (Koptur 2006; Possley et al. 2008; Jones and Koptur 2018; Koptur and Khorsand 2018). The field experiment was conducted over several weeks in May and June of 2010, at Larry and Penny Thompson Park, one of the largest fragments of pine rockland in Miami-Dade County (1.09 km^2, UTM coordinates: 559449 2831668), part of the Richmond Complex (Possley et al. 2018), managed by the county's Natural Areas Management. It is a popular public park with many well-trodden cross-country running trails, picnic areas, and camp-ground facilities. Our study areas were on the southern side, in the largest area of contiguous forest in the park, where *A. berteroi* and all species of palms were abundant.

Experimental Design

We measured flower visitation, pollen deposition, and fruit set, using potted *A. berteroi* grown from seed (collected from this and other pine rockland fragments) in the Florida International University greenhouse, when they were placed in the field near a flowering palm, while others were placed near non-flowering

Figure 1.—Potted *Angadenia berteroi* plants placed in pine rocklands (A) near non-flowering palms; (B) potted plant placed near flowering palm; (C) *A. berteroi* flower; (D) rear end of bee deep in the corolla of *A. berteroi*, probing for nectar.

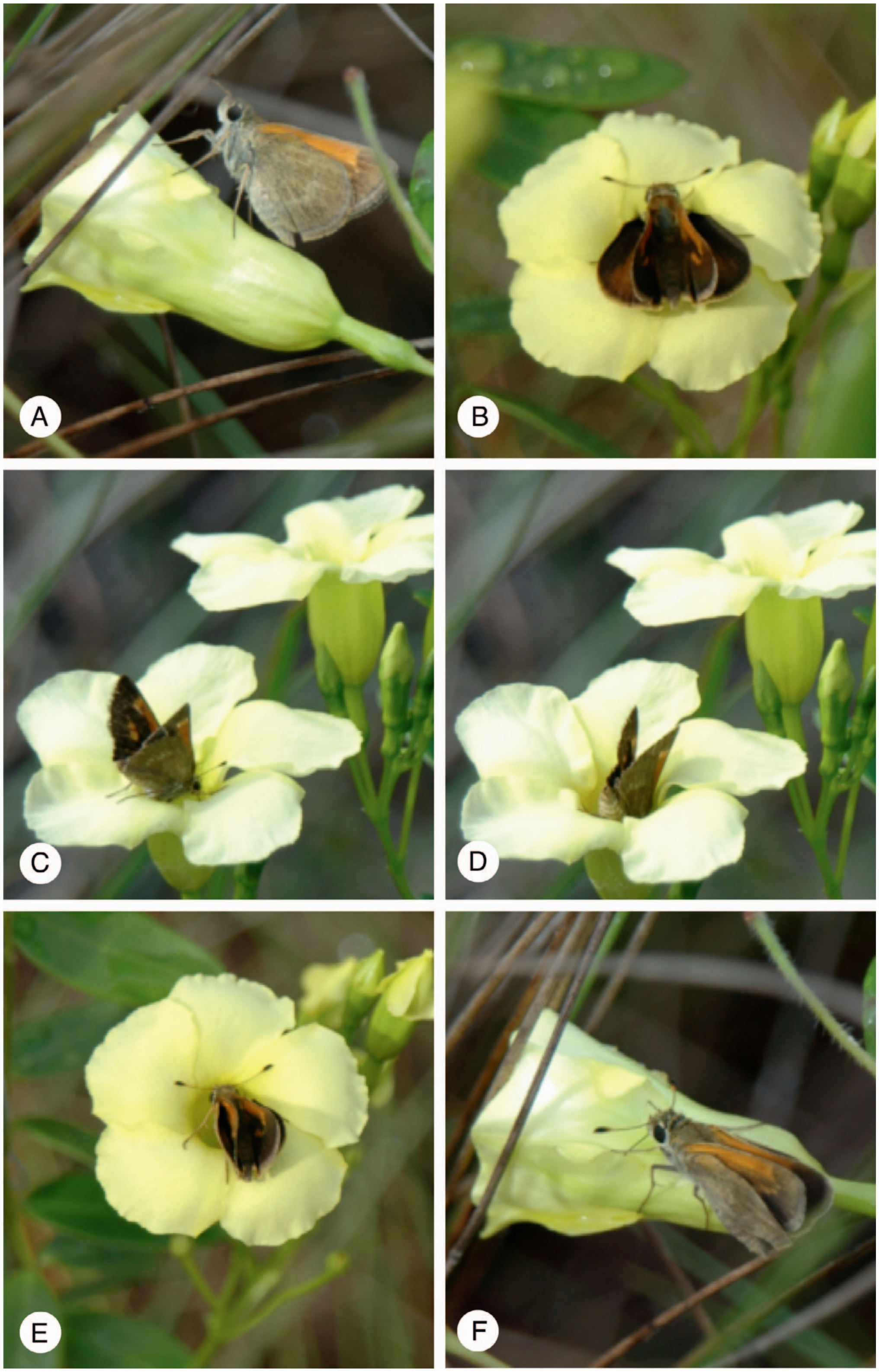

Figure 2.—Baracoa skipper (*Polites baracoa*) visiting flowers of *Angadenia berteroi*: (A) side view of skipper on outside of corolla, (B) landed on corolla mouth, (C) entering bell of corolla, (D) deep in bell, proboscis entering narrow tube at bottom to find nectar, (E) retracting proboscis and retreating from flower, (F) pausing on outside of corolla to wipe proboscis, covered with sticky floral mucilage and pollen.

Table 1.—Visitors to *Angadenia berteroi* flowers on potted plants placed in the field within 12 observation periods of 10 min each by two observers (a total of 240 min over 3 d). *Visitors to palms (last column) compared from this and our previous studies.

Latin name	Common name	Number of visits observed	% of total visits observed	Visitor to palms also?*
Lepidoptera				
Polites baracoa (Lucas)	Baracoa skipper	10	25%	Not seen
Electrostrymon angelia (Hewitson)	Fulvous hairstreak	2	5	Yes
Agraulus vanillae L.	Gulf fritillary	1	3	Not seen but other large butterflies observed
Hymenoptera				
Apis mellifera	Honey bee	6	15	Yes
Melissodes sp.	Leafcutter bee	9	23	Yes
Augochlora sp.		3	8	Yes
Dialictus 2 spp.		5	13	Yes
Pseudomyrmex gracilis (Fabricius)	Elongate twig ant	3	8	Yes
Tiny wasp (indet.)		1	3	?
Total number visits observed		40	100	

palms (Figure 1A, B). We placed 10 or more plants with large flower buds in the field in the afternoon before flower opening. Five plants were placed in separate locations, each near a palm with open flowers (within 5 m of that palm), and the other five were placed in other separate locations near a non-flowering palm individual (within 5 m). Each of the potted plants was located more than 15 m from another of the potted plants, and each day we used different potted plants, and different sites to place them near or far from a flowering palm. Therefore, each potted *A. berteroi* plant examined in the study can be considered independent from the others. We tied colored thread around the pedicel of the flowers that were open each morning and collected the fallen flowers the next morning. Some plants presented more than one open flower on a given day (two or three), and we consider all flowers on each plant individually. We repeated this procedure for 6 d over 2 wk in May, using different plants each day, returning plants placed in the field to the greenhouse daily to monitor fruit set of the exposed flowers. In total, we placed 78 plants in the field, presented 141 and collected 93 flowers near flowering palms and presented 106 and collected 87 flowers near non-flowering palms.

Two stationary observers performed pollinator watches on the potted plants for 10-min intervals every half hour for several morning hours of each day, recording the type of visitor, time on flower, and its movements. We also observed if they touched the reproductive parts of the flower, reporting here only those that did. We then compared the number of flower visitors and number of flower visits for *A. berteroi* plants placed near flowering palms with those for plants placed near non-flowering palms, using simple *t*-tests.

We examined the flowers exposed in the field, recording whether or not pollen had been deposited on the receptive surface area. We carefully dissected and mounted the styles in fuchsin gel to avoid contamination or pollen transfer from the sterile head to the base of the style head where the receptive stigmatic surface is located (Barrios and Koptur 2011). Our sample sizes were equal to the number of flowers collected: near flowering palms ($N = 93$) and near non-flowering palms ($N = 87$). We compared the observed number of stigmas with pollen between the two groups using contingency table χ^2 analysis, with the expectation of equality.

We monitored fruits in the greenhouse, and as they matured, we taped them to prevent the loss of seed when the mature fruit split open. Fruit maturation in *Angadenia berteroi* takes approximately 80 d after pollination (Barrios and Koptur 2011), and these observations lasted until late August 2010. We measured fruit length and counted the number of seeds produced in each fruit. Fruit length was found to correlate with seed number in a previous study (Barrios and Koptur 2011) and confirmed here. We compared fruit set between groups using χ^2 analysis, as above, with the expectation of equality. Fruit lengths were compared using Student's *t*-test.

RESULTS

Visitor Observations

We observed 40 visits to flowers on the potted *A. berteroi* plants over 240 min of watches, an average of one flower visit every 6 min. The majority of flower visits were by the same kinds of butterflies and bees that also visit palm inflorescences, with the exception of the Baracoa skipper, not previously seen to visit palm flowers (Table 1).

Visits to *A. berteroi* flowers were substantially greater for the flowers on plants near non-flowering palms vs. those near flowering palms, a mean of 4.7 vs. 1.2 over 24 observation periods (*t*-test 3.5, $P = 0.003$; Table 2). The number of visitors was much greater to *A. berteroi* flowers on plants near non-flowering palms (2.9 vs. 0.6, *t*-test 5.4, $P < 0.0001$), as was the number of visitor species observed (2.8 vs. 0.6, $t = 5.1$, $P < 0.0001$). The number of flowers observed in the two placement groups during each watch period did not differ significantly ($t = 0.71$, $P = 0.49$).

Pollen Deposition

Examining the mounted styles under the microscope, we recorded the presence or absence of pollen on the stigmatic surface. Even though there was pollen on some of the style heads, this was normal as this species has secondary pollen presentation (Barrios and Koptur 2011); we only counted pollen deposited on the stigmatic surface as evidence of visitation. On some stigmas, we also observed pollen tube growth, evidence of cross-pollination. More flowers near non-flowering palms received pollen on their stigmatic surfaces than did those near

Table 2.—Flower visits to *Angadenia berteroi* potted plants placed in pine rockland habitat. Treatments were NFP (near flowering palm) and NNP (near non-flowering palm). N = number of observation periods; t-test for equality of means for each parameter, equal variance not assumed.

Measurement of visitation	Treatment	N	Mean	Std. dev	Std. error mean	t	Sig. 2-tailed
Number of visits	NFP	12	4.67	3.06	0.882	3.5	0.003
	NNP	10	1.20	1.40	0.442		
Number of visitors	NFP	12	2.92	1.38	0.398	5.4	<0.0001
	NNP	10	0.60	0.52	0.163		
Number of visitor species	NFP	12	2.83	1.40	0.405	5.1	<0.0001
	NNP	10	0.60	0.52	0.163		
Number of flowers observed	NFP	12	4.75	1.91	0.552	0.71	0.49
	NNP	10	4.10	2.33	0.737		

flowering palms (66/87 vs. 55/93; Pearson $\chi^2 = 5.70$, $P = 0.018$; Figure 3).

Plant Reproduction

Fruit set on *A. berteroi* flowers open to visitors in the field in the two placement treatments did not differ significantly from one another (Pearson $\chi^2 = 0.35$, $P = 0.56$; Figure 4). The size of the fruit (the length of the longest follicle) correlates with the number of seeds in the fruit (Barrios and Koptur 2011), but fruit sizes did not differ between treatments.

DISCUSSION

Potential pollinators visited fewer flowers on *Angadenia berteroi* plants near flowering palms, an indication that the abundance of palm flowers offering both nectar and pollen were a greater attraction for visitors than the attractive, but fewer, flowers on our potted experimental *A. berteroi* plants. Lower pollen deposition in these target plants when they were placed near flowering palms demonstrates that the palms are successful competitors for pollinators with native wildflowers in the pine rockland habitat. We observed no significant difference in fruit set, but this may be because the target species, *A. berteroi*, is self-incompatible. Though we found pollen deposited on stigmas in our experiment, it sometimes may have been from flowers on the same plant, as the potted plants were more than 15 m from one another, and this was a time when very few conspecific plants were flowering in the field.

Though it may be presumptuous to assume conclusive demonstration with this one field experiment, coupled with previous observations on other native wildflowers, we suggest that flowering palms are "pollinator hogs" in southern Florida, and perhaps elsewhere. More studies should continue to investigate the role/impact of palms on neighboring flowering plants dependent on pollinators, as many other studies have shown that attractive species may be "magnets" or "hogs," depending on the situation. When the sheer numbers of rewarding flowers overwhelm the senses of floral visitors, as is the case with the large inflorescences of *Sabal palmetto* and *Serenoa repens*, the nearby wildflowers with smaller offerings may be neglected, and plants far from the flowering palms will receive better pollinator services. Our findings have implications for the management of pine rocklands, not only for maintenance of native plant diversity, but pollinators as well.

Improper management of natural areas of pine rockland in south Florida can lead to an overabundance of understory. The main problem is fire suppression, and when the understory of long-unburned pine rockland fills with palm canopies and tall hardwoods, the abundance and reproduction of understory herbs decreases (O'Brien 1998; Barrios et al. 2011, 2016). Our findings that flowering palms hog the floral visitors to *A. berteroi* may have serious negative impacts on the reproduction

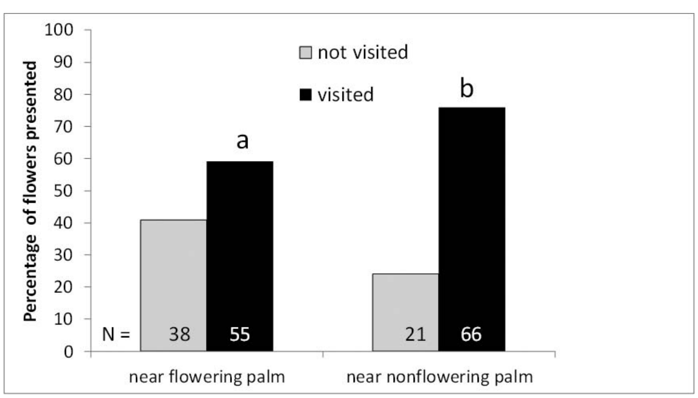

Figure 3.—Pollen deposition comparisons on stigmatic surface of flowers exposed all day near flowering palms ($N = 93$) and near non-flowering palms ($N = 87$). Bars show the percentage of each group with and without pollen observed. Letters above bars show significant differences (Pearson $\chi^2 = 5.70$, $P = 0.018$).

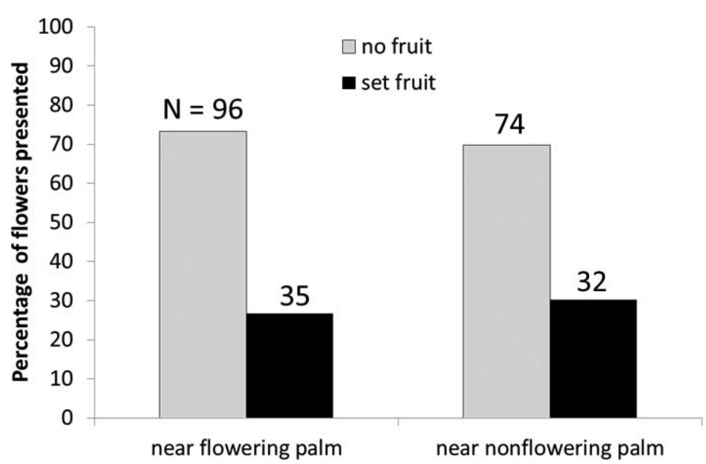

Figure 4.—Fruit set comparisons from flowers exposed all day (same flowers as in Figure 1). Sample sizes are greater here as not all corollas with adherent stigmatic surfaces were recovered, due to loss and herbivory by Orthoptera. Pearson $\chi^2 = 0.35$, $P = 0.56$.

of understory wildflowers and may be especially important to those species that are threatened or endangered. In urban and suburban areas, flowering palms may be very important in the support of pollinating insects, in both habitat fragments and the urban landscape. However, from the perspective of many other species of less abundant flowering plants, the adage "Too much of anything is not a good thing" may hold true for the native palms in the understory of natural areas in southern Florida.

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Suzanne Koptur is Professor of Biological Sciences at Florida International University. A plant ecologist with interests in plant/animal interactions, she and her students focus on species interactions in natural and disturbed habitats. A member of the Pine Rockland Working Group, and the Connect to Protect Network (of Fairchild Tropical Botanic Garden), she is involved in conservation of rare plants and animals, and habitat restoration. She has worked with FIU students and others to create ecological schoolyard and neighborhood habitats in the urban landscape of southern Florida to promote conservation as well as public education.

Beyte Barrios Roque (MS and PhD in Biology, Florida International University) has interests in effects of habitat fragmentation and natural disturbance on animal–plant interactions of the native plants of South Florida pine rocklands, having conducted research in many pine rockland habitat fragments of Miami-Dade County. She works now as an ESE Teacher, teaching Biology, Chemistry, and helping students with learning disabilities to appreciate native ecosystems of central Florida.

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