RESEARCH ARTICLE

Pollination Ecology of Three Sympatric Palms of Southern Florida Pine Rocklands

Suzanne Koptur[1,3]

[1]Florida International University
Department of Biological Sciences and
International Center for Tropical Botany
11200 SW 8th St.
Miami, FL 33199

Roxaneh Khorsand[1,2]

[2]University of Northern Colorado
School of Biological Sciences
501 20th St.
Campus Box 92
Greeley, CO 80639

[3] Corresponding author:
kopturs@fiu.edu; (305) 348-3103

Natural Areas Journal 38:15–25

ABSTRACT: Three native palms are dominant features of the pine rocklands understory of peninsular southern Florida: sabal palm (*Sabal palmetto*), saw palmetto (*Serenoa repens*), and silver palm (*Coccothrinax argentata*). Despite the abundance of these three palm species, the breeding system and pollination mechanisms need further clarification. We used controlled hand-pollination experiments to investigate the breeding systems of these three species. We also observed and captured floral visitors, as well as examined their bodies for pollen, to determine the pollinator assemblages. Our experiments demonstrated that all three palms are self-compatible, and some flowers may set fruit with no manipulation. Natural (open) pollination treatments yielded more fruit than either cross- or self-pollination, indicating no shortage of pollination and suggesting that multiple visits by many pollinators enhances fruit set. We observed a wider variety of visitors (Coleoptera, Diptera, Hymenoptera, Lepidoptera) to flowers of sabal and saw palmetto, as they offer both nectar and pollen. On flowers of silver palm, we observed only pollen-collecting bees. We found evidence of palm flower specialists in only two cases: *Xylocopa* micans bees carried only *Coccothrinax* pollen and *Anartia jatrophae* butterflies carried only *Sabal* pollen. All other visitors appeared to be generalists as they carried pollen from multiple plant species. These results highlight the importance of subcanopy palms in the pine rocklands ecosystem as they provide floral rewards for a wide array of insects that are beneficial for other plants of this imperiled habitat.

Index terms: flowers, insects, palms, pine rocklands, pollination

INTRODUCTION

Palms are dominant and important components of the subtropical pine rocklands and other habitats in Florida (Brown 1973, 1976; Zona 1997; Carrington et al. 2001, 2003; Carrington and Mullahey 2006). Palm nectar and pollen are important food resources for insects; other animals, including black bears (*Ursus americanus* Pallus), small mammals, and birds (Zona 1997), consume palm fruits. Humans harvest honey from honeybees foraging on these palms and collect the fruits of saw palmetto for medicinal purposes (Bennett and Hicklin 1998). Three sympatric palm species (sabal palm [*Sabal palmetto* (Walt.) Lodd. ex J.A. & J.H. Schultes], saw palmetto [*Serenoa repens* (W.Bartram) Small], and silver palm [*Coccothrinax argentata* (Jacq.) L.H.Bailey]) occur in the imperiled pine rocklands of southern peninsular Florida (Figure 1), a habitat greatly reduced in its extent by human development, with only small habitat fragments remaining (Possley et al. 2008).

Pine rocklands are fire-successional habitats with a canopy of slash pine (*Pinus elliottii* Engelm. var. *densa* Little & Dorman) over a subcanopy of palms and hardwoods and a diverse understory of forbs and grasses (Snyder et al. 1990; FNAI 2010). Without fire, hardwoods grow up and overtake the pines to become the climax community of this highest, driest, limestone rocky ground, the hardwood hammock. In southern Florida, pine rocklands occur both on the mainland along the Miami Rock Ridge and in the Lower Keys. The same palm species may be encountered in both pine rockland locations, but Keys pine rocklands have additional palm species abundant (Sah et al. 2006).

More than any other habitat in south Florida, pine rocklands have been targeted for human economic development due to their relatively high elevation (2–7 m above sea level; Snyder et al. 1990; Koptur 2006). As a consequence, this habitat is considered imperiled and a number of its native species are listed as threatened and endangered by state and federal agencies (Gann et al. 2002, 2009; Possley et al. 2008).

The most distinctive members of the understory of subtropical south Florida pine rocklands are palms. They are often the largest plants, overtaken in size only by sparsely dispersed South Florida slash pine. The large leaves of palms grow from a central stem, rather than on woody branches, as is the case for most other understory shrubs. In pine rocklands, palms play a role in nearly every plant/animal interaction, for they are ubiquitous, determining the structure of shade and open areas, as well as providing resources for pollinators and other herbivores with their flowers, leaves, and fruits. Palm leaves provide not only shade for resting animals (such as Key deer [*Odocoileus virginianus clavium* Barbour & Allen]; B. Harris, pers.

Figure 1. Sympatric palms in pine rockland habitat at Navy Wells Preserve. Left, front: *Serenoa repens*; right, front: *Sabal palmetto*; center, behind: *Coccothrinax argentata*.

comm.), but ample combustible fuel for the fires that are essential to maintain the open character of pine rockland habitat (Cooley 2004; Sah et al. 2006). Palms are fire-adapted and normally leaf out soon after a burn, flowering more exuberantly than when the area is unburned (Gunderson et al. 1983). Of the three native species occurring together at most pine rockland sites, two (sabal palm and saw palmetto) are widespread and abundant, and the third (silver palm) is less common but locally abundant at certain sites (Figure 1).

Co-blooming, sympatric species may either compete for pollinators (Stiles 1977; Waser 1978) or share pollinators (Koptur 1983; Moeller 2004). The benefits of sharing may be most important for rare plant species (Schemske 1981; Rathcke and Lacey 1985), which may be able to attract more pollinators when they bloom simultaneously with other species that attract the same visitors (Thomson 1978; Feinsinger et al. 1986; Geber and Moeller 2006). When there is competition for visitors, especially among co-blooming abundant species, many factors involving the dispersal and receipt of pollen could limit fruit set, thereby affecting plant fitness (Mitchell et al. 2009). In patches of abundant, co-blooming species, the number and quality of pollinator visits affect both seed production (female fitness) and seed siring (male fitness). The negative effects of pollinator competition include fewer flower visitations (Campbell 1985) and less conspecific pollen deposition because pollinators groom themselves between visits to other species (Flanagan et al. 2009). Foreign pollen can also interfere with germination of conspecific pollen due to stigma clogging (Waser 1978; Waser and Fugate 1986) or inhibition of pollen germination and fertilization success (Galen and Gregory 1989).

Most previous studies of pollination in pine rocklands have focused on wildflowers or other showy dicotyledonous flowering plants (Pascarella et al. 2001; Liu and Koptur 2003; Koptur 2006; Cardel and Koptur 2010; Linares and Koptur 2010; Downing and Liu 2013). Wildflowers may receive few or no visits when they are adjacent to blooming sabal palms or saw palmettos (Pinto-Torres and Koptur 2009). In the present study, we focused on sabal palm and saw palmetto, along with the less common silver palm, comparing the pollination requirements for fruit set and the floral visitors to each species.

By looking at the plants that make up the "backdrop" for other flowering plants in the pine rockland, we hoped to learn more about these common palms with large, attractive inflorescences, especially the details of their own floral biology, breeding systems, and pollinators. In elucidating what insect visitors are supported by the floral resources that native palms provide, we could learn if and how important they are to overall conservation of plant/animal interactions and ecosystem services of the pine rockland community.

We sought to learn more about their floral morphology and rewards, interactions with floral visitors, and the extent to which they depend upon flower visitors for pollination. We asked if palm flowers need visitors to set fruit, if they can set fruit with their own pollen, and to what extent these three palm species share pollinators with one another and with other sympatric flowering plants of Florida pine rocklands. For the first time, we consider the implications of their sympatry in their pollination ecology, and discuss potential effects on the other species in the habitat. Two of the three species have received detailed attention by researchers in other parts of their range, so our study adds information about their biology in a new geographic location.

METHODS

Study Sites

We conducted the fieldwork from February through May 2008 at one of the larger remaining fragments of pine rockland, the Navy Wells Preserve (1.43 km^2; UTM coordinates: easting 549776, northing 2813432). Additional pollinator observations were made at Larry and Penny Thompson Park (1.09 km^2; UTM easting 559449, northing 2831668). We chose Navy Wells for our experiments since a fire the previous year had incited luxurious regrowth and blooming of understory plants, wildflowers, and palms; the study area in Larry and Penny was similarly recently burned.

Study Species

Sabal palmetto, *Serenoa repens*, and *Coccothrinax argentata* are members of the palm subfamily Coryphoideae. *Sabal* is placed in the tribe Sabaleae; *Serenoa* and *Coccothrinax* are in the tribe Cryosophileae (Dransfield et al. 2008). Flowers of these species are hermaphroditic and are borne on the surface of the rachillae (flower-bearing branches of the inflorescence), rather than sunken in pits, as they are in some other Coryphoideae. Hermaphroditic flowers with many stamens may attract pollen-collecting insects, but the presence of nectaries in both *Sabal* and *Serenoa* suggests insect visitors also seek nectar rewards (Silberbauer-Gottsberger 1990).

Sabal palm is the state tree of Florida, occurring abundantly on rockland substrates. Mature plants are 1–2.5 m in height at our study sites. Leaves are distinctively costapalmate, with a single long fiber hanging off each leaflet margin (often collected by birds as nesting material). The large inflorescences develop over weeks, with individual buds evident long before numerous, small flowers open. *Sabal* species that have been studied have predawn flower opening with production of strong, fragrant odor (Brown 1976; Zona 1987). Brown (1976) found that flowers are protogynous, nectar is produced at the base of the ovary, and bees and flies visit before dawn. Coleoptera and Lepidoptera visit flowers nocturnally, when the flowers are withered (Brown 1976). In a study of flower-visiting Hymenoptera of the Everglades, *Sabal palmetto* was one of two species in Everglades habitats that displayed the greatest species richness of non-apoid floral visitors as well as the greatest number of bee species (Pascarella et al. 2001). Those authors also noted that aggregations of the beetle *Trigonopeltastes delta* (Forster) were attracted to the large inflorescences of sabal palms. Fruits are round, single-seeded berries less than 1 cm in diameter, dark purple to black in color when mature; seeds are shiny and brown (Zona 1990).

Saw palmetto has both prostrate and upright stems. At our study sites, flowering plants are usually less than 1-m tall. The petiole edges of the fan-shaped leaves have saw-like teeth, giving the plant its common name. Flowers are small but numerous, have a strong, sweet fragrance, and produce viscous nectar. Inflorescences develop similarly to those of sabal palm, flowering both after fire in the winter (dry) or the growing (wet) season, but fruiting better with less frequent fire (Carrington and Mullahey 2006). *Serenoa repens* is fire-resistant and increases in abundance with frequency of fires. The greatest flowering is apparent on plants the first year following a fire (Carrington and Mullahey 2013). Hand-pollination experiments by Carrington et al. (2003) demonstrated that saw palmetto flowers set more fruit with insect visitation than without. More than 300 species of insects were observed to visit the flowers (Deyrup and Deyrup 2012; Deyrup 2016). Carrington et al. (2003) reported that the small but numerous flowers last more than one day. Fruits are drupes with a fragile endocarp, up to 2-cm long, bluish black in color and juicy when ripe (Long and Lakela 1971; Zona 1997).

Silver palm is a long-lived, slow-growing palm. Leaves are silvery underneath, giving this species its common name. Although plants flower at less than 1-m high, some individuals reach a height of 2 m or more at our study sites. Two morphotypes have been identified: the shorter, northern morph growing on the mainland (including our sites) and the taller, southern morph growing in the Florida Keys (Davis et al. 2007). Unlike the inflorescences of *Sabal palmetto* and *Serenoa repens*, the inflorescence of *C. argentata* opens suddenly, the rachillae expanding beyond the sheathing bracts to expose all the flowers in anthesis at once. Flowers are small and white, with 7–12 twisted stamens and one carpel. Described as anemophilous (Uhl and Moore 1977; Henderson 1986; Zona 1997), our observations and experiments demonstrated that insects also effectively pollinate the flowers (Khorsand Rosa and Koptur 2009). Silver palm fruits are single-seeded berries, less than 1 cm in diameter, from light purple to black, rarely pink or white, with thick pulp (Long and Lakela 1971; Zona 1997).

Note that, from this point onward, we will refer to the three species by their generic names, for two reasons: to avoid confusion as two genera begin with the same letter, and to use Latin rather than common names to facilitate international understanding.

Controlled Hand-pollination Experiments

We monitored inflorescences to determine how buds grew over time and which buds were likely to open soon so we could bag appropriate inflorescences. We bagged inflorescences (or portions of the inflorescence) using very fine nylon mesh bags with threads less than 0.1-mm apart (breathable, but impenetrable by floral visitors) prior to flower bud opening, so that we protected the newly opened flowers from any animal visits.

We conducted hand-pollinations on *Sabal* and *Serenoa* in the early morning hours, after anthers had dehisced. We collected pollen from newly opened flowers by putting anthers in glassine envelopes, and then applied the pollen to receptive stigmas one time using fine paintbrushes. We replaced the mesh bag, and left it on for 14–21 d, until fruit formed. We did not emasculate (remove stamens) flowers in any of the treatments, so there was self-pollen present inside all the bags, though deliberately applied only in the self-pollination treatment. Our treatments were (1) bagged, no manipulation (to test for automatic self-pollination); (2) bagged, self-pollen applied (to measure fruit set with self-pollination); (3) bagged, cross-pollen applied (from another individual of the same palm species, to measure fruit set with cross-pollination); and (4) control, unbagged, open (natural) pollination (to measure fruit set with no manual treatment but open to floral visitors).

On each inflorescence, we counted the number of rachillae, and on a subsample of each species, we counted the number of flower buds on each rachilla. From these data, we calculated total flower numbers for each inflorescence, which we used to estimate fruit set. For each inflorescence treated (and the control) we noted the number of open flowers that were present and pollinated (or not) at the time of treatment. We counted the number of fruit formed on each inflorescence once they had developed and nearly matured; the bags caught the fruit if they fell before counting.

Because of its all-at-once opening of flowers on an inflorescence, we were not able to hand-pollinate *Coccothrinax*, but we were able to bag inflorescences prior to their opening so that all flowers were bagged on some inflorescences (excluding all floral visitors). We compared fruit set between the unbagged (open) treatment and the bagged treatment to determine if visitors were needed for fruit set.

Since fruit set data were not normally distributed, we used a nonparametric Kruskal–Wallis test to compare fruit numbers and fruit set (percentage) by treatment, and the Mann–Whitney as a post-hoc test for pairwise comparisons. For *Coccothrinax*, with only bagged and open-pollinated inflorescences, we compared fruit set using the Mann–Whitney test. Statistical analyses were performed in IBM SPSS Statistics version 19 (SPSS, Chicago, IL, USA).

Floral Visitors

We watched different individuals for 10-minute observation periods for a total of 120 person-minutes (twelve 10-minute observation periods) for each species of palm, as well as for the abundantly flowering *Metopium toxiferum* (L.) Krug & Urb. (Anacardiaceae) and other wildflowers. We recorded the number of individuals of each visitor type (not species) during every observation period, categorizing the visitors as Coleoptera, Diptera, Hymenoptera (subdivided as bees and wasps), and Lepidoptera. After the observation periods, representatives of each visitor taxon were caught (three to five individuals) and vouchers made for species determination, and to examine the bodies for pollen. We sampled the bodies under a dissecting microscope using insect pins to remove pollen grains from insects and put the pollen collected into fuchsin gel on slides (Dafni et al. 2005). We then compared pollen on the slides with pollen in our reference collection, made from the palms being studied, as well as the other flowering species of the pine rockland. Insect voucher specimens are held in the Koptur lab collection for eventual deposition in the Florida Arthropod Collection at the Florida Museum of Natural History.

RESULTS

Controlled Hand-pollination Experiments

Mean fruit set was low in all *Sabal* and *Serenoa* treatments (1–3%), with the Kruskal–Wallis test not significant among all treatments (df = 3, $P > 0.05$) and Mann–Whitney U also not significant between any pairwise comparison (Figure 2). For *Coccothrinax*, bagged flowers with no visitors displayed little fruit set (7%) compared with those open to visitors (~80%), a highly significant difference with the Mann–Whitney test ($U = 6.0$, $P < 0.0001$).

Floral Visitors

We observed at least 30 species of arthropods associated with flowers of the three palm species: 27 floral visitors (Table 1), and 3 floral herbivores (Table 2). Two of the herbivorous insects are generalist feeders, known to eat the leaves and flowers of other species in this habitat (Figure 3). *Pachnaeus litus* (Germar), citrus root weevil, feeds on leaves and flowers of cultivated citrus and other fruit trees, as well as on leaves of native plants (Peña et al. 2003; Koptur et al. 2015). Caterpillars of the echo moth have been observed eating a wide array of pine rockland plants, from gymnosperms (*Zamia pumila* L.; Negron-Ortiz and Gorchov 2000) to wildflowers (Cardel and Koptur 2010). Only the cabbage palm caterpillar is somewhat specialized on palms, though not as specialized as its name might imply, as it was also found on saw palmetto and silver palm in our study. Four species of floral visitors were observed on all three palms: love bugs (*Plecia nearctica* Hardy), honeybees (*Apis mellifera* L.), graceful twig ants (*Pseudomyrmex gracilis* Fabricius), and the Georgian leafcutter bee (*Megachile georgica* Cresson). At least 10 species were observed visiting only *Sabal* and *Serenoa* flowers (and not *Coccothrinax*), including six bees, two beetles, a wasp, and a moth; at least 16 species were shared between the two species (Table 1). Only one species was observed uniquely on *Coccothrinax* flowers in our study: the carpenter bee, *Xylocopa micans* Lepeletier (Figure 4). We found three species of bees collecting pollen from *Coccothrinax*.

We estimated the relative importance of each visitor group from the numbers of recorded observations. Bees are the most frequent group of visitors to all the palms at the study sites, as well as to *Metopium toxiferum* (L.) Krug & Urb. (poisonwood) and wildflowers in bloom during our experiments (Figure 5). The greatest number of Lepidoptera (butterflies and moths) were observed on *Sabal*, followed by *Serenoa*; they were less abundant on wildflowers in general and infrequently seen on *Metopium*. We never observed Lepidoptera on *Coccothrinax* flowers. Coleoptera were most numerous on *Serenoa*, and never observed on *Coccothrinax*. We observed Diptera visiting flowers of all three palms, on *Metopium*, and on some other wildflowers, but at low frequency.

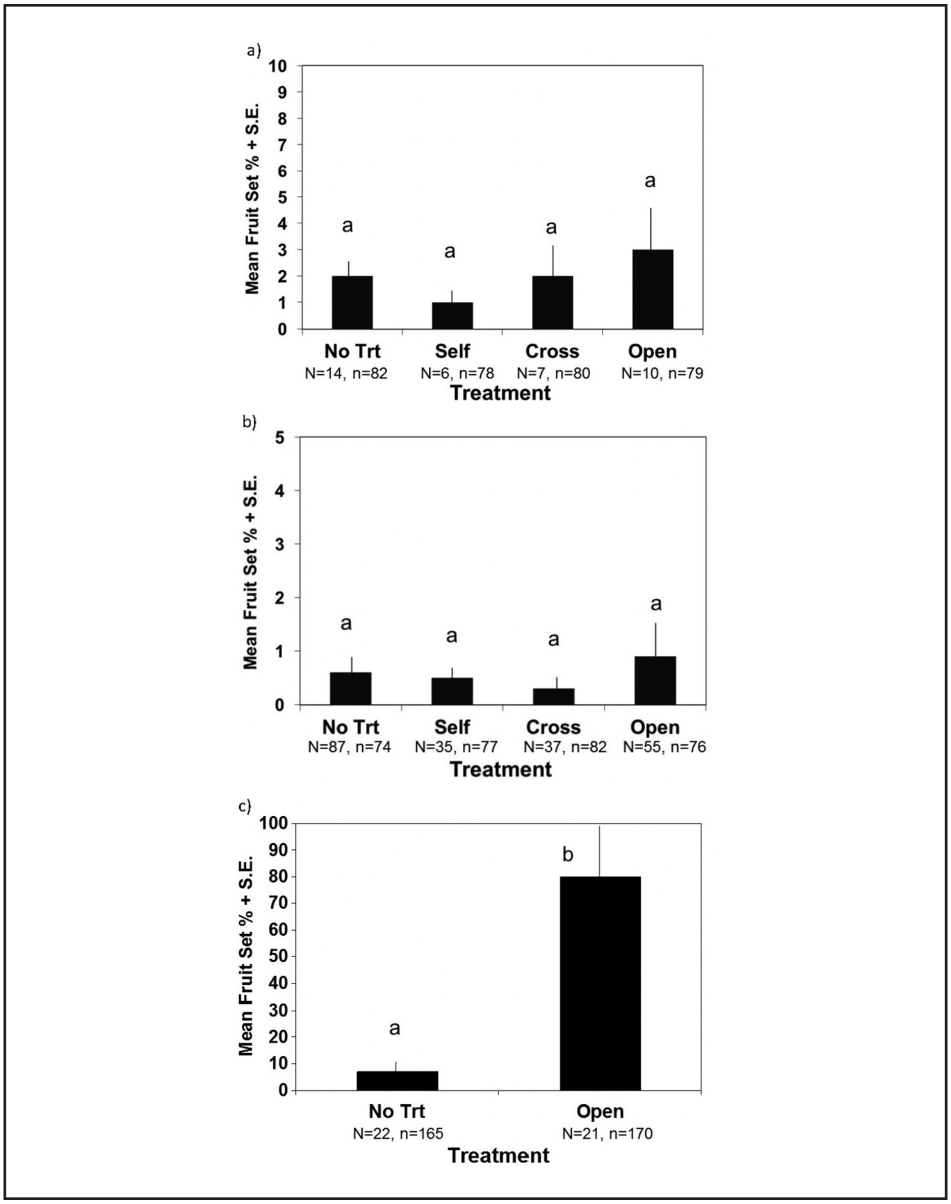

Figure 2. Fruit set from hand-pollination experiment (a: *Sabal palmetto*; b: *Serenoa repens*) and pollinator exclusion experiment (c: *Coccothrinax argentata*) conducted at Navy Wells Preserve. No treatment = no pollen applied by hand, inflorescence bagged. Self = pollen from same individual applied to stigmas of open flowers, inflorescence bagged. Cross = pollen from different individual applied to stigmas of open flowers, inflorescence bagged. Open = no pollen applied by hand, inflorescence not bagged, open to natural visitation. N = number of inflorescences for each treatment, n = average number of flowers per treatment.

All visitors collected from palm inflorescences had palm pollen on their bodies. It was common to find Hymenoptera and Lepidoptera with both palm and wildflower pollen on their bodies. Many individuals had loads with *Sabal*, *Serenoa*, and one or more species of wildflower pollen, including *Ruellia succulenta* (J.F.Gmel.) Steud., *Angadenia berteroi* (A. DC.) Miers, *Centrosema virginianum* (L.) Benth., and *Solidago stricta* Aiton. The most common non-palm pollen observed on visitors was that of a woody species abundant at the sites, *Metopium toxiferum* (L.) Krug & Urb. (poisonwood). The flowers of this species glisten with nectar and evidently attract a wide variety of insects. Visitors were likely collecting nectar from the palms and non-palms alike, though it is possible that some were collecting pollen from wildflowers and poisonwood as well. *Coccothrinax* pollen is smaller than *Sabal* and *Serenoa* pollen (Figure 6), and some of the bees had nearly pure loads of *Coccothrinax* pollen after visiting its flowers. As *Coccothrinax* flowers offer no nectar, we can be sure that the purpose of their visits was to collect pollen. It was not possible for us to distinguish *Sabal* pollen from that of *Serenoa* using our simple fuchsin gel technique, as they are quite similar in size and shape.

DISCUSSION

Henderson (1986) and Barfod et al. (2011) showed that this subfamily of palms displays a diversity of pollination syndromes: beetle pollinated (with persistent bracts covering the rachillae at anthesis) and bee pollinated (without persistent bracts). *Sabal*, *Serenoa*, and *Coccothrinax* do not have persistent bracts, falling into the bee-pollinated category, according to those authors. The flowers of the three pine rockland palms received many kinds of insect visitors, including butterflies, moths, flies, and beetles, as well as bees. While bees account for more than half of the visits, these other insects likely provide pollination services as well.

Our observations demonstrate that palms of the pine rocklands share many floral visitors. Pollinator sharing may not be disadvantageous to any one species if flowers and visitors are numerous. Petit (2011) saw no detrimental effects of co-blooming in columnar cacti in Curacao, and natural pollination yielded more fruit than hand-pollinations in her experiments. In tropical dry forests of Costa Rica, flowering peaks in the dry season, where flowers produced on mostly leafless trees easily attract visitors looking for water and sugars provided by nectar, and most trees receive ample pollination (Frankie et al. 1974). Though seasonality in south Florida is not as dramatic, during the later months of the dry season in the pine rocklands, the flowering palms provide abundant resources of nectar and pollen at a time most other flowering plants are also in bloom. Nevertheless, we saw neither evidence of reduced fitness from pollinator sharing, nor evidence that other plants in bloom (poisonwood, wildflowers, etc.) had any

Table 1. Flower visitors to inflorescences of three pine rockland palm species, as well as to the flowers of poisonwood (*Metopium toxiferum*) and to other common wildflowers at two pine rockland sites in Miami-Dade County, Florida.

Flower visitor Latin name / common name	Visitor order/family	*Coccothrinax argentata*	*Sabal palmetto*	*Serenoa repens*	*Metopium toxiferum*	Other wildflowers
Euphoria sepulchralis (Fabricius) / flower beetle	Coleoptera: Scarabaeidae		X	X	X	X
Trigonopeltastes delta (Förster) / Delta flower scarab	Coleoptera/Scarabaeidae		X	X		X
Plecia nearctica Hardy / Love bugs	Diptera/Bibionidae	X	X	X	X	X
Flies – spp. undetermined	Diptera		X	X		X
Apis mellifera L. / honey bee	Hymenoptera/Apidae	X	X	X	X	X
Augochlora pura Cockerell ssp. *mosieri*	Hymenoptera/Halictidae		X	X	X	X
Augochlorella gratiosa Smith	Hymenoptera/Halictidae		X	X	X	X
Augochloropsis anonyma Cockerell	Hymenoptera/Halictidae		X	X	X	X
Campsomeris trifasciata Saussure	Hymenoptera/Scoliidae		X	X	X	X
Camponotus floridanus (Buckley) / carpenter ant	Hymenoptera/Formicidae		X	X	X	X
Camponotus rasilis Wheeler	Hymenoptera/Formicidae		X	X		
Centris errans Fox	Hymenoptera/Apidae			X		X
Dialictus tegularis (Robertson)	Hymenoptera/Halictidae		X	X		X
Dianthidium curvatum Smith	Hymenoptera/Megachilidae		X	X		X
Halictus ligatus Say	Hymenoptera/Halictidae			X		X
Megachile albitarsis Cresson	Hymenoptera/Megachilidae		X	X		
Megachile georgica Cresson	Hymenoptera/Megachilidae	X	X	X		X
Megachile pruina pruina Smith	Hymenoptera/Megachilidae		X			
Melissodes communis Cresson	Hymenoptera/Anthophoridae		X			X
Pachodynerus erynnis (Lepeletier)	Hymenoptera/Vespidae			X		X
Pseudomyrmex gracilis Fabricius	Hymenoptera/Formicidae	X	X	X		X
Xylocopa micans Lepeletier / carpenter bee	Hymentopera/Apidae	X				X
Vespid wasps sp. undet.	Hymenoptera/Vespidae		X			
Anartia jatrophae L. / white peacock butterfly	Lepidoptera/Nymphalidae		X			
Eurema dina (Poey) / Dina yellow	Lepidoptera/Pieridae			X		
Pseudocharis minima (Grote)	Lepidoptera/Arctiidae			X		X
Syntomeida ipomoeae Harris / yellow-banded wasp moth	Lepidoptera/Arctiidae		X			X
Utetheisa bella (L.) / Bella moth	Lepidoptera/Arctiidae		X	X	X	X

Table 2. Floral herbivores observed consuming flowers of three pine rockland palm species in pine rocklands of Miami-Dade County, Florida.

Floral herbivore	Order/family	*Coccothrinax argentata*	*Sabal palmetto*	*Serenoa repens*
Pachnaeus litus (Germar) – citrus root weevil	Coleoptera/ Curculionidae		X	X
Seirarctia echo (J.E. Smith) – echo moth caterpillars	Lepidoptera/ Arctiidae	X	X	X
Litoprosopus futilis Grote & Robinson – cabbage palm	Lepidoptera/ Noctuidae	X	X	X

detrimental effect on the palms.

Interspecific competition can reduce fruit set in some situations and can reduce the amount of outcrossing, lowering seed quality in species as a direct result of competition (Bell et al. 2005). There is potential for competition among the palms for pollinators, but during our observation periods, there were numerous visitors on all inflorescences. We found no evidence for pollen limitation in *Sabal* and *Serenoa*, given the lack of statistical difference in fruit set between the treatment and control. We were surprised with the very low fruit set we observed in all treatments and our controls, but perhaps the temperatures or rainfall during our study had some negative effects. It may simply be that with the enormous numbers of flowers in their inflorescences, the palms still make quite a lot of fruit even with a relatively small proportion of their flowers setting fruit. The rates of natural self- vs. cross-pollination, as well as the relative success of fruits derived from self- vs. cross-pollination, merit further investigation.

All of the palm species investigated appear to be self-compatible, as fruit from self-pollinations was set in both *Sabal* and *Serenoa*, and a small number of fruit was set in flowers that were simply bagged in *Coccothrinax*. Studying Bromeliaceae in Brazil, Matallana et al. (2010) suggested that self-pollination may function as a reproductive isolating mechanism among co-blooming, sympatric species, facilitating fertilization by conspecific and identical individuals. The palms, belonging to separate genera, are not known to hybridize and no intergeneric hybrids are known between any of these species. It is more likely that genetic barriers to hybridization, rather than extensive self-pollination, are the reproductive isolating mechanisms at play.

Sympatric related species may have displaced flowering periods, as in bat-pollinated *Parkia* spp. in Amazonian Brazil (Hopkins 1984), perhaps to reduce competition. Alternatively, related species may open their flowers at different times of the day, minimizing interference with one another, as in *Acacia* spp. in Africa (Stone et al. 1998) and in seasonal tropical forests of Mexico (Raine et al. 2007) or *Inga* spp. in cloud forests of Costa Rica (Koptur 1983). Such separation of flowering times was not observed in these palms of pine rocklands, as they all bloomed prolifically and simultaneously at our study sites.

In some situations, sympatric related species share pollinators simultaneously, but deposit pollen on different parts of the pollinator's bodies. In species of *Trichostema* (Lamiaceae), pollen is deposited on a bee's abdomen or thorax, dorsal or ventral surface, depending on the size of the bee and the way it visits the flowers of each species, resulting in spatial partitioning of pollen types on the pollinators' bodies (Spira 1980). Likewise, co-blooming *Helleborus* (Ranunculaceae) species in Italy have different floral forms and bees (*Bombus* spp.) visit them in different ways, resulting in specialized placement

Figure 3. Floral herbivores occurring on all three palm species (left to right): *Seirarctia echo* – echo moth caterpillars (Lepidoptera/ Arctiidae); *Pachnaeus litus* – citrus root weevil (Coleoptera/Curculionidae); and damage by *Litoprosopus futilis* Grote & Robinson – cabbage palm caterpillar (Lepidoptera/ Noctuidae) shown here on saw palmetto, *Serenoa repens*.

Figure 4. Floral visitors (clockwise, from upper left): *Augochloropsis anonyma* on *Sabal palmetto; Dianthidium curvatum* on *Serenoa repens, Apis mellifera* on *Coccothrinax argentata, Xylocopa micans* on *Coccothrinax argentata* (evidently not just wind-pollinated) – and in the center, *Metopium toxiferum* (poisonwood).

of pollen loads (Vesprini and Pacini 2010). The small, radially symmetric flowers of similar size in our study species do not provide the morphological features that would allow this sort of differentiation in pollen placement; indeed, pollen loads on the bodies of most visitors were mixed.

Shared pollinators may restrict their visits to one species or another due to individual preferences, as is the case with oligolectic bees (e.g., *Perdita* specializing in Boraginaceae; Portman et al. 2016), or due to territoriality restricting pollinator movement, as in hummingbirds and Andean Solanaceae (Smith et al. 2008). Other floral visitors may prefer to visit only one species of flower at a time (displaying floral constancy). The fact that we observed only one type of pollen on some of the collected visitors suggests that one or more of these restrictions might be the case for certain taxa, such as *Xylocopa* bees visiting only *Coccothrinax*. The flowering strategy of *Coccothrinax* (many flowers, all opening at once) is most effective when pollinator loyalty is high; the abundance of their pollen may encourage short-term specialization by *Xylocopa* bees, often seen to be generalists, visiting many other kinds of flowers.

As human population has increased in southern Florida, the pine rockland habitat has become increasingly fragmented (Snyder et al. 1990; Koptur 2006; Barrios et al. 2011). Although it is a challenge to have fires in small parcels of fragmented pine rockland habitat, fire is important in controlling overgrowth of both native and exotic hardwoods (Possley et al. 2014). A healthy pine rockland flora depends on periodic fires, and it is evident that without these disturbances many endemic species decline in abundance (O'Brien 1998; Liu et al. 2005; Barrios et al. 2011; Barrios et al. 2016; Possley et al. 2016). Like many other perennial species in this fire-succesional habitat, palms survive and resprout vigorously, with growth and flowering enhanced by nutrients released from the burned vegetation after periodic fires (Cooley 2004; Sah et al. 2006).

Palms are certainly important in other southern ecosystems; Abrahamson (2016) calls palmettos growing in the sandy soils of the scrub habitat "foundation species," as they play a major role in structuring the community. In pine rocklands, our observations support their role as foundation species of the understory, with a large influence on the many animals with which they associate, that are in turn associated with many other plant species in this diverse habitat.

Our study demonstrates (as has work by many others) the important role that flowering palms play in attracting and sustaining a panoply of visitors. The three palms found in pine rocklands of peninsular south

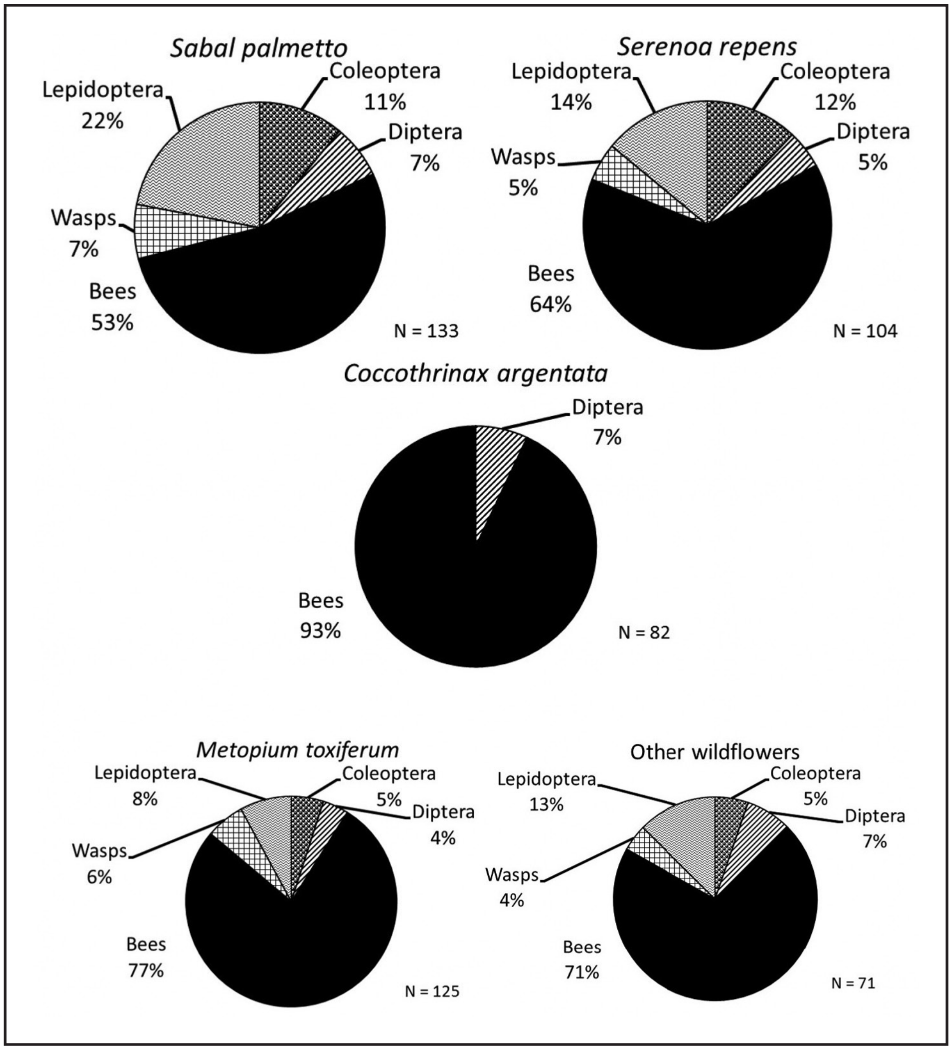

Figure 5. Flower visitors to flowers of the three pine rockland palm species, *Metopium toxiferum*, and to other wildflowers at Navy Wells Preserve. Proportions of the total number of individual visitors of each group observed on each during a total of 120 minutes over multiple 10-minute observation periods.

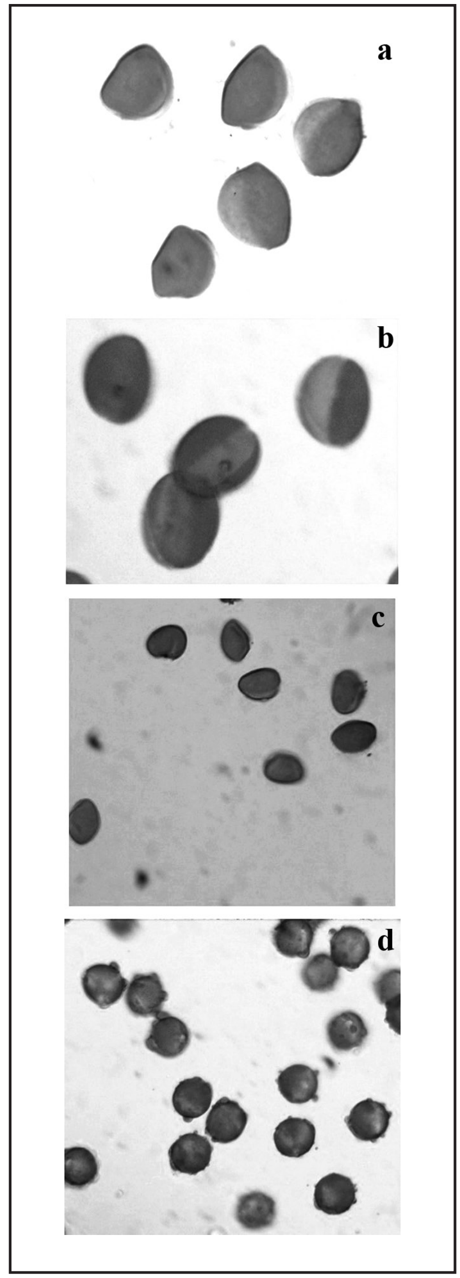

Figure 6. (a) Sabal palmetto pollen is slightly larger (30–40 × 25–30 microns) than (b) *Serenoa repens* pollen (25 × 30 microns) and both are visibly larger than (c) *Coccothrinax argentata* pollen (20 × 30 microns). The other pollen most commonly found on visitors, that of (d) poisonwood (*Metopium toxiferum*) is similar in size to that of *C. argentata*, but has tiny oil droplets visible on the surface of the pollen grains.

Florida exhibit extended flowering seasons, and in all species the individuals of the population do not flower synchronously, providing a relatively constant source of pollen and nectar for insects of the pine rocklands. Further work examining the impact of palm flowering on pollination of flowers of other pine rockland plant species may reveal both positive and negative effects.

ACKNOWLEDGMENTS

We thank Michelle Barragan, Adel Peña, and Nuno Rosa for field assistance, and Miami-Dade Natural Areas Management for granting permission to work in pine rockland sites (under permit #0080). Dr. Scott Zona has been an invaluable resource for palm biology, and provided constructive comments on the manuscript, as did Brittany Harris, Jaeson Clayborn, Adel Peña, Cleopatra Pimienta, Imeña Valdes, and two anonymous reviewers. This is contribution number 348 to the Tropical Biology Program of Florida International University.

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 south Florida to promote conservation as well as public education.

Roxaneh Khorsand is a Visiting Assistant Professor at the University of Northern Colorado. Her previous research has focused on plant reproductive ecology in Amazonian Brazil as well as the Alaskan Arctic, investigating the effects of the abiotic environment and climate change on plant phenology and pollination success. Currently, she and her students are studying phenotypic plasticity and plant–pollinator interactions in the sub-alpine biome of the Rocky Mountains, with the aim of predicting species-specific and ecosystem responses to climate change. Roxaneh enjoys sharing her passion for plant ecology and the natural world through outreach with children in rural and urban schools in Brazil, south Florida, and Colorado.

LITERATURE CITED

Abrahamson, W.G. 2016. A tale of two palmettos: The foundation of ecosystems. Palmetto 33:4-7.

Barfod, A.S., M. Hagen, and F. Borchsenius. 2011. Twenty-five years of progress in understanding pollination mechanisms in palms (Arecaceae). Annals of Botany 108: 1503-1516.

Barrios, B., G. Arellano, and S. Koptur. 2011. The effects of fire and fragmentation on occurrence and flowering of a rare perennial plant. Plant Ecology 212:1057-1067.

Barrios Roque, B., S. Koptur, and J.P. Sah. 2016. The effects of habitat fragmentation on the reproduction and abundance of *Angadenia berteroi*. Journal of Plant Ecology 10:340-348.

Bell, J.M., J.D. Karron, and R.J. Mitchell. 2005. Interspecific competition for pollination lowers seed production and outcrossing in *Mimulus ringens*. Ecology 86:776-785.

Bennett, B.C., and J. Hicklin. 1998. Uses of *Serenoa repens* (Bartr.) Small (saw palmetto) in Florida. Economic Botany 52:365-375.

Brown, K.E. 1973. Ecological life history and geographical distribution of the cabbage palm, *Sabal palmetto*. PhD diss., North Carolina State University, Raleigh.

Brown, K.E. 1976. Ecological studies of the cabbage palm, *Sabal palmetto*. Principes 20:3-10.

Campbell, D.R. 1985. Pollinator sharing and seed set of *Stellaria pubera*: Competition for pollination. Ecology 66:544-553.

Cardel, Y., and S. Koptur. 2010. Effects of florivory on the pollination of flowers: An experimental field study with a perennial plant. International Journal of Plant Science 171:283-292.

Carrington, M.E., T.D. Gottfried, and J.J. Mullahey. 2003. Pollination biology of saw palmetto (*Serenoa repens*: Palmae) in southwest Florida. Palms 47:95-103.

Carrington, M.E., and J.J. Mullahey. 2006. Effects of burning season and frequency on saw palmetto (*Serenoa repens*) flowering and fruiting. Forest Ecology and Management 230:69-78.

Carrington, M.E., and J.J. Mullahey. 2013. Saw palmetto (*Serenoa repens*) flowering and fruiting response to time since fire. Rangeland Ecology & Management 66:43-50.

Carrington, M.E., P.D. Roberts, N.V.R.R. Urs, R.J. McGovern, T.E. Seijo, and J.J. Mullahey. 2001. Premature fruit drop in saw palmettos caused by *Colletotrichum gloeosporioides*. Plant Disease 85:122-125.

Cooley, H.C. 2004. Palm fuel dynamics in fire sustained pine forests in the Florida Keys. MS thesis, Florida International University, Miami.

Dafni, A., P.G. Kevan, and B.C. Husband. 2005. Practical Pollination Biology. Enviroquest, Ltd. Cambridge, Ontario, Canada.

Davis, A., C. Lewis, J. Francisco-Ortega, and S. Zona. 2007. Differentiation among insular and continental populations of *Coccothrinax argentata* (Arecaceae): Evidence from DNA markers and a common garden experiment. Taxon:103-111.

Deyrup, M. 2016. Saw palmetto flowers are a biodiversity bonanza. Palmetto 33:12-14.

Deyrup, M., and L. Deyrup. 2012. The diversity of insects visiting flowers of saw palmetto (Arecaceae). Florida Entomologist 95:711-730.

Downing, J., and H. Liu. 2013. Self-incompatibility in *Byrsonima lucida* (Malpighiaceae), a threatened pine rockland specialist. Castanea 78:95-102.

Dransfield, J., N.W. Uhl, C.B. Asmussen, W.J. Baker, M.M. Harley, and C.E. Lewis. 2008. Genera Palmarum: The Evolution and Classification of Palms. Kew Publishing, Richmond, Surrey, UK, in association with the International Palm Society and the L.H. Bailey Hortorium, Cornell University, Ithaca, NY.

Feinsinger, P., K.G. Murray, S. Kinsman, and W.H. Busby. 1986. Floral neighborhood and pollination success in four hummingbird-pollinated cloud forest plant species. Ecology 67:449-464.

Flanagan, R.J., R.J. Mitchell, D. Knutowski, and J.D. Karron. 2009. Interspecific pollinator movements reduce pollen deposition and seed production in *Mimulus ringens* (Phrymaceae). American Journal of Botany 96:809-815.

[FNAI] Florida Natural Areas Inventory. 2010. A guide to the natural communities of Florida. Florida Natural Areas Inventory and Florida Department of Natural Resources, Tallahassee.

Frankie, G.W., H.G. Baker, and P.A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62:881-919.

Galen, C., and T. Gregory. 1989. Interspecific pollen transfer as a mechanism of competition: Consequences of foreign pollen contamination for seed set in the alpine wildflower, *Polemonium viscosum*. Oecologia 81:120-123.

Gann, G.D., Bradley, K.A., and S.W. Woodmansee. 2002. Rare Plants of South Florida: Their History, Conservation, and Restoration. The Institute for Regional Conservation, Delray Beach, FL.

Gann, G.D., K.A. Bradley, and S.W. Woodmansee. 2009. Floristic Inventory of South Florida Database. Institute for Regional Conservation, Delray Beach, FL.

Geber, M.A., and D.A. Moeller. 2006. Pollinator responses to plant communities and implications for reproductive character evolution. Pp. 102-119 *in* L.D. Harder and S.C. H. Barrett, eds., The Ecology and Evolution of Flowers. Oxford University Press, Oxford, UK.

Gunderson, L., D. Taylor, and J. Craig. 1983. Fire effects on flowering and fruiting patterns of understory plants in pinelands of Everglades National Park. Report SFRC-83/04, National Park Service, South Florida Research Center, Everglades National Park, Homestead.

Henderson, A. 1986. A review of pollination studies in the Palmae. Botanical Review 52:221-259.

Hopkins, H. 1984. Floral biology and pollination ecology of the neotropical species of *Parkia*. Journal of Ecology 72:1-33.

Khorsand Rosa, R., and S. Koptur. 2009. Preliminary observations and analyses of pollination in *Coccothrinax argentata*: Do insects play a role? Palms 53:75-83.

Koptur, S. 1983. Flowering phenology and floral biology of *Inga* (Fabaceae: Mimosoideae). Systematic Botany 8:354-368.

Koptur, S. 2006. The conservation of specialized and generalized pollination systems in subtropical ecosystems: A case study. Pp. 341-361 *in* N. Waser and J. Ollerton, eds., Plant–Pollinator Interactions: From Specialization to Generalization. University of Chicago Press, Chicago, IL.

Koptur, S., I.M. Jones, and J.E. Peña. 2015. The influence of host plant extrafloral nectaries on multitrophic interactions: An experimental investigation. PLOS One e0138157.

Linares, L.J., and S. Koptur. 2010. Floral biology and breeding system of the crenulate lead plant, *Amorpha herbacea* var. *crenulata*, an endangered south Florida pine rockland endemic. Natural Areas Journal 30:138-147.

Liu, H., and S. Koptur. 2003. Breeding system and pollination of a narrowly endemic herb of the lower Florida Keys: Impacts of the urban–wildland interface. American Journal of Botany 90:1180-1187.

Liu, H., E.S. Menges, J.R. Snyder, S. Koptur, and M.S. Ross. 2005. Effects of fire intensity on vital rates of an endemic herb of the Florida Keys, USA. Natural Areas Journal 25:71-76.

Long, R.W., and O. Lakela. 1971. A Flora of Tropical Florida. University of Miami Press, Coral Gables, FL.

Matallana, G., M.A.S. Godinho, F.A.G. Guilherme, M. Belisario, T.S. Coser, and T. Wendt. 2010. Breeding systems of Bromeliaceae species: Evolution of selfing in the context of sympatric occurrence. Plant Systematics and Evolution 289:57-65.

Mitchell, R.J., R.J. Flanagan, B.J. Brown, N.M. Waser, and J.D. Karron. 2009. New frontiers in competition for pollination. Annals of Botany 103:1403-1413.

Moeller, D.A. 2004. Facilitative interactions among plants via shared pollinators. Ecology 85:3289-3301.

Negron-Ortiz, V., and D. Gorchov. 2000. Effects of fire season and postfire herbivory on the cycad *Zamia pumila* (Zamiaceae) in slash pine savanna, Everglades National Park, Florida. International Journal of Plant Sciences 161:659-669.

O'Brien, J.J. 1998. The distribution and habitat preferences of rare *Galactia* species (Fabaceae) and *Chamaesyce deltoidea* subspecies (Euphorbiaceae) native to southern Florida pine rockland. Natural Areas Journal 18:208-222.

Pascarella, J.B., K.D. Waddington, and P.R. Neal. 2001. Non-apoid flower-visiting fauna of Everglades National Park, Florida. Biodiversity and Conservation 10:551-556.

Peña, J.E., J. Sharp, and M. Wysoki. 2003. Tropical Fruit Crops: Pests and Pollinators. CAB International, Wallingford, UK.

Petit, S. 2011. Effects of mixed-species pollen load on fruits, seeds, and seedlings of two sympatric columnar cactus species. Ecological Research 26:461-469.

Pinto-Torres, E., and S. Koptur. 2009. Hanging by a coastal strand: Breeding system of a federally endangered morning-glory of the south-eastern Florida coast, *Jacquemontia reclinata*. Annals of Botany 104:1301-1311.

Portman, Z.M., J.L. Neff, and T. Griswold. 2016. Taxonomic revision of *Perdita* subgenus *Heteroperdita* Timberlake (Hymenoptera: Andrenidae), with description of two antlike males. Zootaxa 4214:1-97.

Possley, J., S. Hodges, E. Magnaghi, and J. Maschinski. 2016. Distribution of *Croton linearis* in Miami-Dade County preserves with potential for supporting the federally endangered butterflies *Strymon acis bartrami* and *Anaea troglodyta floridalis*. Natural Areas Journal 36:81-87.

Possley, J., S.W. Woodmansee, and J. Maschinski. 2008. Patterns of plant composition in fragments of globally imperiled pine rockland forest: Effects of soil type, recent fire frequency, and fragment size. Natural Areas Journal 28:379-394.

Possley, J.E., J.M. Maschinski, J. Maguire, and C. Guerra. 2014. Vegetation monitoring to guide management decisions in Miami's urban pine rockland preserves. Natural Areas Journal 34:154-165.

Raine, N.E., A.S. Pierson, and G.N. Stone. 2007. Plant–pollinator interactions in a Mexican *Acacia* community. Arthropod-Plant Interactions 1:101-117.

Rathcke, B., and E.P. Lacey. 1985. Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics 16:179-214.

Sah, J.P., M.S. Ross, J.R. Snyder, S. Koptur, and H.C. Cooley. 2006. Fuel loads, fire regimes, and post-fire fuel dynamics in Florida Keys pine forests. International Journal of Wildland Fire 15:1-16.

Schemske, D.W. 1981. Floral convergence and pollinator sharing in two bee-pollinated tropical herbs. Ecology 62:946-954.

Silberbauer-Gottsberger, I. 1990. Pollination and evolution in palms. Phyton 30:213-233.

Smith, S.D., C. Ané, and D.A. Baum. 2008. The role of pollinator shifts in the floral diversification of *Iochroma* (Solanaceae). Evolution 62:793-806.

Snyder, J.R., A. Herndon, and W.B. Robertson Jr. 1990. South Florida rockland. Pp. 230-280 *in* R.L. Myers and J.J. Ewel, eds., Ecosystems of Florida. University of Central Florida Press, Orlando.

Spira, T.P. 1980. Floral parameters, breeding system and pollinator type in *Trichostema* (Labiatae). American Journal of Botany 67:278-284.

Stiles, G. 1977. Coadapted competitors: The flowering seasons of hummingbird-pollinated plants in a tropical forest. Science 198:1177-1178.

Stone, G.N., P. Willmer, and J.A. Rowe. 1998. Partitioning of pollinators during flowering in an African *Acacia* community. Ecology 79:2808-2827.

Thomson, J.D. 1978. Effects of stand composition on insect visitation in two-species mixtures of *Hieracium*. American Midland Naturalist 100:431-440.

Uhl, N., and H.E. Moore. 1977. Correlations of inflorescence, flower structure and floral anatomy with pollination in some palms. Biotropica 9:170-190.

Vesprini, J.L., and E. Pacini. 2010. Pollination ecology in sympatric winter flowering *Helleborus* (Ranunculaceae). Flora 205:627-632.

Waser, N.M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. Ecology 59:934-944.

Waser, N.M., and M.L. Fugate. 1986. Pollen precedence and stigma closure: A mechanism of competition for pollination between *Delphinium nelsonii* and *Ipomopsis aggregata*. Oecologia 70:573-577.

Zona, S. 1987. Phenology and pollination biology of *Sabal etonia* (Palmae) in southeastern Florida. Principes 31:177-182.

Zona, S. 1990. A monograph of *Sabal* (Arecaceae: Coryphoideae). Aliso 12:583-666.

Zona, S. 1997. The genera of Palmae (Arecaceae) in the southeastern United States. Harvard Papers in Botany 2:71-107.