

ANTS AND PLANTS WITH EXTRAFLORAL NECTARIES IN FIRE SUCCESSIONAL HABITATS ON ANDROS (BAHAMAS)

SUZANNE KOPTUR, PASCALE WILLIAM AND ZURIANY OLIVE

Department of Biological Sciences, Florida International University, Miami, FL 33199

E-mail: kopturs@fiu.edu

ABSTRACT

Honey baits were used to assess the activity and abundance of nectar-drinking ants in fire successional habitats of rocklands on Andros Island, Bahamas. Vegetation was sampled in pineyard and coppice habitats (the same communities as Florida's pine rocklands and hammocks), revealing a larger proportion of taxa with extrafloral nectaries in coppice samples, but roughly equivalent cover of plants with extrafloral nectaries in pineyard and coppice vegetation. Ant activity was greater in pineyard than in coppice habitats, with time to discovery of baits the shortest in open and recently burned pineyards, and most of the baits experiencing recruitment of ants. Overgrown pineyards and coppices both had longer time-to-discovery and much less recruitment to baits; coppice edges, more variable, were not significantly different from either of the 2 other habitat groups. Our preliminary study revealed some new records of plant genera and species with extrafloral nectaries, but all ants we observed at nectaries and on baits are also known from pine rocklands and hardwood hammocks of south Florida.

Key Words: extrafloral nectaries, ant-plant interactions, ants, Bahamas, Caribbean, fire, mutualism, rocklands

RESUMEN

Se utilizaron cebos con miel para determinar la actividad y abundancia de hormigas nectarívoras en habitats sucesionales que sufrieron incendios en suelos rocosos (malpais) de la Isla Andros, en Bahamas. La vegetación fue muestreada en pinares y habitats de coppice (lo mismo comunidades que los pinares rocosos y hammocks de Florida), revelando un número mayor de taxa de plantas con nectarios extraflorales en las muestras de coppice, y casi igual cobertura de plantas con nectarios extraflorales en la vegetación de pinar. Asimismo, la actividad de las hormigas fue mayor en el pinar que en el coppice, siendo las zonas abiertas y recientemente incendiadas del pinar las que presentaron los menores tiempos de descubrimiento de los cebos por las hormigas y la mayoría de los cebos experimentaron reclutamiento de hormigas en estos sitios. Los pinares más altos (con daño menos reciente por fuego) presentaron tiempos mayores en el descubrimiento de los cebos por las hormigas y mucho menor reclutamiento; los bordes de los coppice, fueron mas variables y no resultaron significativamente diferentes de ninguno de los otros grupos de hábitats. Nuestro estudio preliminar reveló muchos nuevos registros de géneros y especies con nectarios extraflorales, pero todas las hormigas que nosotros observamos en los nectarios y en los cebos son también especies conocidas de los pinares rocosos y los hardwood hammocks del sur de Florida.

Translation provided by the authors.

Extrafloral nectaries are plant glands occurring in nearly one-third of terrestrial plant taxa (Koptur 1992a; Rogers 1985), a useful food resource with ants, and often associated with these and other beneficial insects (Rogers 1985; Nuessley et al. 2004; Koptur 2005). Plants with extrafloral nectaries have served as model systems for many investigations of plant/animal interactions (Bronstein 1998; Heil & McKey 2003; Rico-Gray & Oliveira 2007) and tests of ecological theory (Holland et al. 2009). Ant abundance limits the range of plants with extrafloral nectaries in some ecosystems (Goitia &

Jaffee 2009), but whether plants benefit or not from ant protection via their extrafloral nectaries may depend on whether the plant is in the sun or in the shade (Kersch & Fonseca 2005), or whether ant-tended herbivores are also present (Koptur & Lawton 1988; Suzuki et al. 2004; Oliver et al. 2007). Sometimes aggressive bodyguards attracted to extrafloral nectaries can interfere with pollinator activity (Ness 2006), and in other plants, while nectaries and ants visiting them may change the insect community on the plant, herbivory experienced by the plant may be unaffected (Mody & Linsenmair 2004).

Plants bearing extrafloral nectaries are more common in tropical than temperate areas; plants with extrafloral nectaries (EFNS) double every 10 degrees latitude when moving from the tundra to the subtropics (Pemberton 1998), and are of intermediate occurrence in the subtropics (Koptur 1992b). Many studies have been undertaken around the world to determine which species have extrafloral nectaries and what proportion of the flora, and extent of vegetation cover, has nectaries (Pemberton 1998; Diaz-Castelazo et al. 2004; Oliveira & Freitas 2004). These surveys have often led to more detailed morphological and anatomical work examining the position and structure of the nectaries (Diaz-Castelazo et al. 2005; Machado et al. 2008) as well as inspired ecological experimentation on their significance and role in particular plants (Sousa e Paiva et al. 2001; Cuautle & Rico-Gray 2003; and many others). Extrafloral nectaries and ant-guards can respond to the environment: their presence can vary among leaves of the same individual, as well as differ among individuals (as in aspen, Doak et al. 2007; Wooley et al. 2007; or peach, Mathews et al. 2009). Furthermore, many recent studies have shown that nectar production can be inducible, as well as the number and size of nectaries on individual plants influenced by damage the plant experiences (Heil 2008), the soil in which the plant grows (Abdala-Roberts & Marquis 2007), and the nutrient status of the plant (Mondor et al. 2006). More nectar leads to greater protection and less herbivory (Kost & Heil 2005).

This study is a contribution to the ongoing world survey of diversity and abundance of plants with extrafloral nectaries, the ants with which they are associated, as well as an assessment of their importance in different habitats of the Bahamas. The Bahamas archipelago lies east of peninsular Florida, and shares some geological and climatic features with southern Florida. While ants of the Bahamas have been studied by few investigators (Morrison 2002), and the islands' plants are fairly well known (Correll & Correll 1982; Morrison 2003; Morrison & Spiller 2008), there have not yet, to our knowledge, been any systematic surveys of plants with extrafloral nectaries in the Bahamas. In a study of plants with extrafloral nectaries and ant activity in upland habitats of the Everglades (Koptur 1992b), the potentially protective interaction was found to be more common in plants of fire-successional pine rocklands than in hardwood hammock or short-hydroperiod glade habitats. In the Bahamas we find similar habitats bearing different names: pine rocklands are called 'pineyard', and hammock is 'coppice'.

Andros is the largest island of the Bahamas archipelago, which has the greatest cover of pine forest of any of the islands. All of the islands were logged in the early-mid twentieth century, with

most of the large diameter pines removed by the 1950s (Henry 1974; Allan 1986), as the modest-diameter trunks of the present-day forest will attest. While wildfires may start via lightning, especially at the beginning of the wet season (Snyder et al. 1990), it is very likely that much of the fire during most of the year is anthropogenic in origin, and Bahamian pine forests have a frequent surface fire regime (O'Brien et al. 2006). Burning brings tender vegetation as the plants resprout, and such areas are desirable for grazing and foraging by wildlife, which may, in turn, be hunted for food. The relationship between fire and pineyard vegetation is relatively clear, as in analogous pine rocklands of southern Florida, where suppression of fire results in forest succession to broad-leaved, hammock vegetation in only 25 years (Robertson 1955; Loope et al. 1994); however, the impact of fire on pineyard insects is not well known.

The objectives of this study were to assess the abundance and activity of nectar-drinking ants that might be associated with plant nectaries, and to systematically observe the plants of different vegetation types to discover which species bear extrafloral nectaries. We measured ant activity in fire successional habitats of Andros, and sampled vegetation to compare the species richness and cover of plants with extrafloral nectaries in these habitats. Our goal was to see how ants and plants with extrafloral nectaries vary among fire successional pineyard and climax coppice habitats on limestone substrates on Andros.

MATERIALS AND METHODS

Study Sites

We chose representative pineyard and coppice sites on the island of Andros, the largest of the 35 inhabited islands in the Bahamas archipelago (Smith & Vankat 1992). The pine rockland (pineyard) habitats occur on 3 of the other islands of the Bahamas: Grand Bahama, Abaco, New Providence, and also on the Caicos Islands (Correll & Correll 1982). Andros is 45 km wide and 165 km long, and divided by shallow channels into 3 main sections; our work was conducted on North Andros. Andros has the greatest expanse of pine forests, and though all were logged throughout the Bahamas in the middle of the twentieth century, they have been left mostly intact, in contrast to the pine rocklands of southern Florida which are now greatly reduced in size due to development. "Open pineyard" and "coppice edge" transects were sampled on the road to Church's blue hole; overgrown pineyard was studied on Love Hill, as was burned pineyard (burned within the previous week, some parts still smoking); and coppice transects were done in Forfar coppice.

Similar to southern Florida, the substrate of Andros is oolitic limestone, with poorly developed soil (Sealey 1985). Karstic weathering in rocklands produces pitted or honeycombed rock surfaces, along with solution holes or sinkholes that may extend down to the freshwater lens below (Smith & Vankat 1992). Andros is 210 km east southeast of Miami, and its annual rainfall (1300 mm) is similar, though slightly less, to that of Miami (1340 mm). The dry evergreen forest communities (coppices) on Andros are more similar to hardwood hammocks of south Florida (with more than one-third of species in common), and to the northern and central islands of the Bahamas, than to the drier, southern islands.

Ants

Ant activity has frequently been assessed by discovery of and recruitment to baits placed in transects in the habitat. Baiting uses food to attract foraging ants to spots where they may be observed and collected (Bestelmeyer et al. 2000), and is an indication of ant abundance and especially, the willingness of ants to take advantage of foods, in a given habitat. We placed 20 honey baits on small white cards (2 cm × 2 cm) on the surface of the ground at intervals of approximately 1.5 m in 1 or 2 linear transects at each site. Honey is similar to nectar in composition, and therefore we expected to measure the activity of nectar-drinking ants, as has been done in earlier studies (Koptur 1985; Koptur & Lawton 1988; Koptur 1992b).

We monitored the baits for 1 h, checking them at 5-min intervals, and recording the presence of ants and other arthropods. We counted the number of each type of ant present (more than 10 individuals of 1 species were recorded as “many”) at each interval for each bait. If any ant found the bait, it was designated “discovered”; if more than 5 individuals of the same species were observed at a bait, that bait was designated as experiencing “recruitment”. We collected specimens of each type at the end of the hour, and tallied the mean time-to-discovery for each bait, as well as the proportion of baits discovered, and the proportion to which there had been recruitment, for each habitat.

We employed univariate analysis of variance (ANOVA) to compare time to discovery among sites (habitats, their ecotone, and different times since fire for pineyards). We therefore had 4 degrees of freedom (5 habitat types minus 1). Because group sizes were unequal, the harmonic mean of the sample size for each group was used. We used post-hoc Tukey HSD and Dunnett C tests to detect significant differences among habitats (SPSS 2002).

The number of baits discovered in each transect/habitat were compared with the Pearson

chi-square test $df = 4$ (5 habitats). Recruitment data (many zero values) were arcsine transformed prior to analysis.

Plants

In each of the 2 main habitat types (pineyard and coppice) we assessed plant species richness along linear transects. Transects of 40 m were laid out (3 in each habitat), and vegetation (an individual plant or plants) intercepted by the transect was recorded for 1 m every 5 m along the transect. We examined the plants carefully to detect the presence of extrafloral nectaries on all surfaces of leaves, stems, and reproductive parts, utilizing hand lenses and dissecting microscopes to determine if these structures were present. We utilized previous knowledge of families and genera to guide our inspections, and in genera and species with which we had no previous experience, we were especially observant, though we may have missed some nectaries with our 1-season sample if the plants were not in the right developmental stage. Additionally, some nectaries are merely pores with no discernible structure and we may have missed those if they were not actively secreting nectar. We collected vouchers of species we could not determine in the field, and were able to determine most of them later using keys and descriptions in floras (Correll & Correll 1982; Patterson & Stevenson 1977).

We compared the proportion of individuals encountered with nectaries, and the proportion of species with nectaries, for each transect. For 2 of the samples, only the total number of species and species with nectaries were recorded (numbers of individuals not recorded). The data in the table therefore represent only 2 transects per habitat for individual counts.

RESULTS

We found 9 species (in 6 genera) of ants visiting extrafloral nectaries and/or honey baits in pineyards and coppices on Andros (Table 1). All of these ant species occur in south Florida (Deyrup 2003; Deyrup et al. 1988), but none of them occurs in either Georgia (Ipser et al. 2004) or in longleaf pine savannahs of Louisiana (Colby & Prowell 2006). Several of the species (*Monomorium ebeninum*, *Paratrechina* spp., *Wasmannia auropunctata*) are exotics that occur throughout the tropics and are considered “tramp species” (Wetterer et al. 1999; Solomon & Mikheyev 2005).

Baits were discovered more quickly in open and recently burned pineyards than in coppices or overgrown pineyards (Fig. 1); coppice edges (the ecotone with pineyards) were not substantially different from either of the other groups. Only in recently burned pineyards were all baits (every single one) discovered within the hour baiting pe-

TABLE 1. BAHAMAS ANTS AND LOCATIONS ENCOUNTERED—ANDROS ISLAND MARCH 2004. ALL SPECIES DETERMINATIONS CONFIRMED BY MARK DEYRUP.

Species	Pineyard	Coppice	Baits	Plants
<i>Brachymyrmex obscurior</i>	X		X	X
<i>Camponotus</i> sp.*	X		X	
<i>Cyphomyrmex minutus</i>		X	X	X
<i>Monomorium eberinum</i>	X	X	X	X
<i>Paratrechina bourbonica</i>	X		X	X
<i>Paratrechina longicornis</i>	X	X		X
<i>Pseudomyrmex cubaensis</i>	X		X	X
<i>Pseudomyrmex</i> sp.*	X		X	
<i>Wasmannia auropunctata</i>	X	X	X	X

*not possible to determine as material was insufficient.

riod; the majority of baits in open pineyard and coppice edge were also discovered within the hour. All baits being discovered within the hour is not unusual in tropical lowland sites (Koptur 1985), but the mean time to discovery of 10 min for burned pineyard was notably rapid. Substantially fewer baits were discovered in coppice and overgrown pineyards (Table 2). All baits placed in recently burned pineyard recruited ants, while roughly half the baits in open pineyard and coppice edge habitats did so. Recruitment is of interest, because more ants may provide more protection, beneficial to plants presenting nectar. In overgrown pineyard and coppice habitats, only one-tenth of the baits successfully recruited ants

(Table 2). Flies were not observed at baits at the site with the highest ant recruitment (recently burned pineyard, with 100% discovery and 100% recruitment), but all other sites had 10-20% of the baits with fly visitors. The flies were not collected, and so are not determined here; some nectar-drinking flies may be beneficial to plants with extrafloral nectaries, as predators or parasitoids.

Of the 83 species of plants encountered in transects in both habitats (pineyard and coppice), we found 23 species with extrafloral nectaries (28% of all species encountered). Pineyards, the fire successional, more open habitat, had a greater total number of species than did coppices (52 vs. 39 spp., in our samples), but a smaller proportion of these species bear extrafloral nectaries (13 species, or 25% for pineyard, vs. 12 species, or 31% for coppice, Table 3). Taking into account the number of individuals encountered in our samples, however, gives a closer percentage occurrence of plants (roughly, cover of plants) with extrafloral nectaries. Pineyards, with 18% of individuals bearing nectaries, have roughly the same proportion of individuals with nectaries, versus 20% cover of plants with nectaries in coppices.

Twelve families of plants (11 angiosperms, and 1 fern) are represented in our sampling by individuals bearing extrafloral nectaries (Table 4). None of the family occurrences are novel, but the presence of extrafloral nectaries has not been previously noted in the genus *Sachsia* (Asteraceae), or in the genus *Petitia* (Verbenaceae). Many of the other species, in genera known to have extrafloral nectary bearing species, are new species occurrences, not surprising as this is a new area for a survey of nectary occurrence (Table 4).

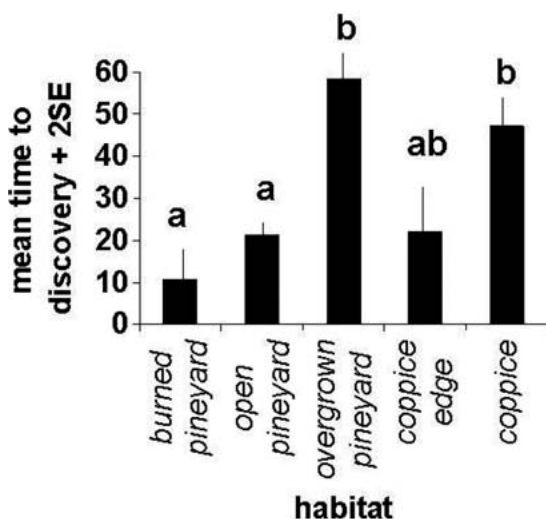


Fig. 1. Mean time to discovery of honey baits in Andros forest habitats. Greater time to discovery indicates lower ant activity. Univariate ANOVA $F(4,1) = 14.888$ $P < 0.0001$. Different letters represent significantly different times to discovery with post-hoc test ($P < .05$); bars with the same letters are not significantly different from each other.

DISCUSSION

Rocklands may seem less hospitable to ants than habitats with sandy soil substrates, where ants can more easily excavate to construct their nests, but rocklands have soil pockets and many fissures in which ants can nest, as well as at the

TABLE 2. SUMMARY OF ANTS AT HONEY BAITS ON ANDROS ISLAND. PERCENTAGE OF 20 BAITS MONITORED FOR 1 H EXPERIENCING DISCOVERY BY ANTS, RECRUITMENT BY ANTS, AND PRESENCE OF FLIES. THE BURNED PINEYARD SITE HAD BEEN BURNED WITHIN THE PREVIOUS WEEK.

	Burned pineyard	Open Pineyard	Overgrown pineyard	Coppice edge	coppice
Discovery (% baits discovered)	100%	90%	20%	90%	50%
Recruitment (% baits with recruitment)	100%	48%	10%	54%	10%
% with flies	0%	22%	10%	18%	10%

TABLE 3. OCCURRENCE OF PLANT SPECIES AND INDIVIDUALS WITH EXTRAFLORAL NECTARIES IN THE 2 MAIN HABITATS ON ANDROS, BAHAMAS. DATA FROM ALL TRANSECTS WERE COMBINED FOR EACH HABITAT.

Habitat	# Spp. encountered in sampling	% Species with extrafloral nectaries (# species)	# Individuals encountered in sampling	% Individuals with extrafloral nectaries (# individuals)
Pineyard	52	25% (13)	256	18% (46)
Coppice	39	31% (12)	177	20% (35)

bases of trees and in trunks and branches of woody vegetation. Fire is so frequent in pineyards of Andros that they are recurrently disturbed, never having the chance for succession to proceed to coppice vegetation. The cover of plants with extrafloral nectaries was similar in pineyards and coppices, though the actual proportion of species with nectaries recorded in pineyards was lower than in coppices. We measured greater ant activity in pineyard than in coppice habitat, and greatest by far in recently burned pineyard habitat. These observations concur with those made in south Florida pine rocklands and hammocks (Koptur 1992b) as well as those in Mexican coffee plantations and cloud forests, where the structure of shade vegetation affects ant species richness, diversity, and abundance: richness and diversity increased with more complex arboreal structure, but abundance decreased (Valenzuela-Gonzalez et al. 2008). We observed the same trends in species richness, and the lower proportions of baits discovered and experiencing recruitment in overgrown pineyard and coppice habitats provides support for the decreased abundance of ants in vegetation with more complex structure. At sea-level in Jamaica, 28% of plants had extrafloral nectaries (Keeler 1979), comparable to our results for these sea-level Bahamian rockland habitats.

Because we used only ground baiting with honey, and not other methods of ant collection (Bestelmeyer et al. 2000), we do not have a complete picture of ant occurrence in these habitats. We may have missed ant species that move from plant to plant without walking on the ground, or those that do not consume nectar, for example. The wider the variety of sampling methods used, the greater the number of species; King & Porter (2005) found that combinations of sampling meth-

ods were much more effective for assessing species richness than any single method.

Our observations on very recently burned pineyards provided us with some surprising results. With virtually no plant cover of any kind in burned pineyard, the ants were hungry, and quickly discovered, and then recruited to honey baits. The ground-nesting Cuban parrots on Abaco were not adversely affected by pineyard fires (O'Brien et al. 2006). Lower fuel loads from frequent fires may keep fire intensity low enough to not endanger nestlings, and parrot pairs choose new nesting sites in recently burned areas. Ant nests may be even deeper than parrot nests, so ant populations that nest below ground may not be harmed by fires. Ant species that nest in trees or near the soil surface are more likely to be reduced by fire. Fire can increase species diversity of plants and some insects (O'Dowd & Gill 1984), but Sanders (2004) found that exotic argentine ant numbers were reduced by 75% following fires in northern California. Ants may be used to monitor environmental change (Kaspari & Majer 2000) but responses to fire will differ for different ant species, influenced especially by where they nest. Several studies have come to different conclusions, but all concur that effects of fire are habitat-dependent (Farji-Brener et al. 2002; Hoffman 2003; Parr et al. 2004; Ratchford et al. 2005). Studies on savannas in Africa (Parr et al. 2002) and Australia (Hoffmann 2003) showed unburned areas to have the lowest species richness and abundance of ants. Our study is in agreement with these general findings, as were data in a similar study in south Florida (Koptur 1992b), where the successional fire habitats (pineyards and pine rocklands) have greater abundance of plants with extrafloral nectaries, and nectar-drinking ants as well.

TABLE 4. PLANT SPECIES WITH EXTRAFLORAL NECTARIES ENCOUNTERED IN SAMPLING PINEYARD AND COPPICE HABITATS ON ANDROS ISLAND, BAHAMAS.

FAMILY	Latin name, authority	common name	Nectary position
Asteraceae	<i>Sachsia polycephala</i> Griseb.*		foliar, phyllaries
Bromeliaceae	<i>Tillandsia balbisiana</i> J. A. & J. H. Schult.	Cuttlefish	Inflorescence—along peduncle and pedicels
	<i>Tillandsia recurvata</i> L.	thread-leaved wild pine	Inflorescence—as above
Chrysobalanaceae	<i>Chrysobalanus icaco</i> L.	Cocoplum	Foliar—abaxial surface near leaf base
Euphorbiaceae	<i>Chamaesyce (Euphorbia) blodgettii</i> Engelm. Ex Hitchc.		Inflorescence, in cyathium
	<i>Croton linearis</i> Jacq.*	granny-bush	Paired on leaf bases, abaxial surface
	<i>Euphorbia heterophylla</i> L.	Jacob's ladder, Governor Grant's Livery	inflorescence
	<i>Grimmeodendron eglandulosum</i> (A. Rich.) Urb.*	young manchineel	leaf base
	<i>Hippomane mancinella</i> L.	Manchineel	petiolar
Fabaceae	<i>Acacia choriophylla</i> Benth.*	Cinnacord	On rachis between leaflets
	<i>Calliandra haematomma</i> (Bert.) Benth.*	red calliandra	foliar
	<i>Cassia nictitans</i> L. var. <i>aspera</i> (Ell.) T. & G.	winking cassia	petiolar
	<i>Lysiloma sabcu</i> Benth.*	Horseflesh	On rachis
	<i>Pithecellobium hystrix</i> (A. Rich.) Benth.*	bristly cat's-claw	On rachis
	<i>Vigna luteola</i> (Jacq.) Benth.	yellow vigna	Inflorescence—abortive floral buds
Malpighiaceae	<i>Stigmaphyllon sagraeanum</i> A. Juss.		foliar
Passifloraceae	<i>Passiflora suberosa</i> L.	corky-stem passionflower, juniper-berry	petiolar
Polypodiaceae	<i>Pteridium aquilinum</i> (L.) Kuhn var. <i>caudatum</i> (L.) Sadebeck	southern bracken	Foliar—where frond becomes ternate and along midrib
Rosaceae	<i>Prunus myrtifolia</i> (L.) Urb.	West Indian Laurel-cherry	Leaf bases
Rubiaceae	<i>Morinda royoc</i> L.	wild mulberry, rhubarb, mouse's pineapple	Postfloral—on ovary after corolla falls off

*Indicates new record of extrafloral nectaries in the species or genus.

TABLE 4. (CONTINUED) PLANT SPECIES WITH EXTRAFLORAL NECTARIES ENCOUNTERED IN SAMPLING PINEYARD AND COPPICE HABITATS ON ANDROS ISLAND, BAHAMAS.

FAMILY	Latin name, authority	common name	Nectary position
Simaroubaceae	<i>Simarouba glauca</i> DC	paradise tree	Foliar—adaxial leaflet surfaces
Verbenaceae	<i>Pettitia domingensis</i> Jacq.*	fowlberry, bastard stopper	abaxial leaf surface

*Indicates new record of extrafloral nectaries in the species or genus.

Five species of Euphorbiaceae and 6 species of Fabaceae occurred in the habitats studied, and have extrafloral nectaries; both are families in which the occurrence, form, and function of nectaries have been well documented (Keeler 2008). *Grimmeodendron* may be a new genus record of extrafloral nectaries for the Euphorbiaceae, and this genus has foliar nectaries on the leaf blade base, similar to those occurring in species of *Alchornea* (Fiala & Linsenmair 1995), and some *Croton* species (Fiala & Maschwitz 1981). In the genus *Croton*, *C. linearis* is a new species in this genus in which foliar nectaries are well known. Nectaries of *Chamaesyce*, in which nectaries occur in the inflorescence, as in *Euphorbia* (So 2004) and *Poinsettia*, but are morphologically extrafloral (the cyathium being comprised of individual flowers of gynoeceium or androeceium only) might function in pollination as well as potential anti-herbivore defense, depending on the ecological context.

In the Fabaceae, cinnacord (*Acacia choriophylla*, a rare endemic in the Florida Keys) has the inter-leaflet foliar nectaries characteristic of many mimosoid legumes, and is a new species record for this genus, in which many ant-plant interactions have been studied, ranging from obligate (Janzen 1966, 1967) to facultative (Whitney 2004). Some ant acacias native to Central America have different, local ant inhabitats when they grow in Florida (Wetterer & Wetterer 2003). *Calliandra haematomma* and *Lysiloma sabicu* have the same type of extrafloral nectaries, probably active on the developing leaves during the time they are the most vulnerable to herbivory; these nectaries may support the same kinds of ant protectors that are present on *Inga* species (Koptur 1984, 1994; Wickers 1997; Pascal et al. 2000), that do not live in the plant but visit constantly for nectar and deter herbivores on the leaves. These other legume species reported from Andros are all additions to the world list (Keeler 2008), the most striking being the spiny, tiny-leaved, large-flowered *Pithecellobium hystrix*, with one nectary on each of its small, twice-compound leaves. The nectaries in the inflorescence of *Vigna luteola* (also occurring in south Florida) are actually abortive flower buds (Kuo & Pate 1985; Pate et al. 1985; Mizell 2004), and support a round-the-clock ant guard that may protect the flowers and fruits from predators (S. Koptur, personal observations).

Many of the other species bearing extrafloral nectaries occur also in south Florida, where very similar rockland habitats occur. *Passiflora suberosa*, *Prunus myrtifolia*, *Pteridium aquilinum*, *Morinda royoc*, and *Simarouba glauca* are all native to Everglades habitats. *Passiflora* leaves and petioles bear extrafloral nectaries that are well known for their support of ant bodyguards and other mutualists that benefit the plants (Smiley

1985; Apple & Feener 2001). *Prunus* nectaries attract ants and also parasitoids that can control herbivores and benefit the plants, increasing their fruit production (Tilman 1978; Pemberton 1990; Pemberton & Lee 1996). *Pteridium* is widespread, and is the single most studied fern with nectaries; in some cases, it appears that ants do not protect the plants though nectaries are functioning to attract the ants (Tempel 1983; Rashbrook et al. 1993); in others, they do (Heads 1986). The nectaries of these ferns may primarily function to deter colonization by new herbivores (Heads & Lawton 1984). *Morinda* has postfloral nectaries (Keeler 1985; Koptur 1992b) that may promote protection of developing fruit as in some Loasaceae (Keeler 1981).

The extrafloral nectaries of *Sachsia* may function as those of other Asteraceae, to attract and maintain ant-guards to deter pre-dispersal seed predators (e.g., *Helianthella quinquenervia*, Inoué & Taylor 1979; *Helichrysum* spp., O'Dowd & Catchpole 1983; *Melanthera aspera*, Mexzon & Chinchilla 1999). This genus occurs in south Florida, Cuba, and the Bahamas (Liu et al. 2004) and merits closer examination.

Petitia, as many other Verbenaceae (species of *Citharexylum*, *Petrea*, and *Stachytarpheta*), bears its extrafloral nectaries on its lower leaf surface (Diaz-Castelazo et al. 2004). To our knowledge, there are not yet any ecological studies on members of this family.

Further observations throughout the year and in more habitats and on more of the islands of the Bahamas will perhaps reveal additional species with nectaries, and very likely more species of ants visiting nectaries and associated with these plants. There may be lower diversity in plants with extrafloral nectaries and ants due to island effects; it will be interesting to make comparisons among islands in the Bahamas and other locations in the Greater and Lesser Antilles. Obviously, antiherbivore defense and other beneficial interactions may well be supported by extrafloral nectaries on plants in Bahamas rockland habitats, and we predict that they will be more important in pineyards than in coppices.

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REFERENCES CITED

- ABDALA-ROBERTS, L., AND MARQUIS, R. J. 2007. Test of local adaptation to biotic interactions and soil abiotic conditions in the ant-tended *Chamaecrista fasciculata* (Fabaceae). *Oecologia* 154: 315-326.
- ALLAN, T. G. 1986. Management plan for the pine forests of the Bahamas. UTF/BHA/003/BHA Consultancy Report No. 2. Food and Agriculture Organization of the United Nations.
- APPLE, J. L., AND FEENER, D. 2001. Ant visitation of extrafloral nectaries in *Passiflora*: the effects of nectary attributes and ant behavior on patterns in facultative ant plant mutualisms *Oecologia* 2001: 409-416.
- BESTELMEYER, B. T., AGOSTI, D., ALONSO, L. E., BRANDAO, C. R. F., BROWN, JR., W. L., DELABIE, J. H. C., AND SILVESTRE, R. 2000. Field techniques for the study of ground-dwelling ants, pp. 122-144 *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz (eds.), *Ants: Standard Methods for Measuring and Monitoring Biodiversity*. Smithsonian Institution Press, Washington.
- BRONSTEIN, J. L. 1998. The contribution of ant plant protection studies to our understanding of mutualism. *Biotropica* 30: 150-161.
- COLBY, D., AND PROWELL, D. 2006. Ants (Hymenoptera: Formicidae) in wet longleaf pine savannas in Louisiana. *Florida Entomol.* 89: 266-269.
- CORRELL, D. S., AND CORRELL, H. B. 1982. Flora of the Bahama archipelago: including the Turks and Caicos Islands. *Vaduz: J. Cramer*.
- CUAUTLE, M., AND RICO-GRAY, V. 2003. The effect of wasps and ants on the reproductive success of the extrafloral nectaried plant *Turnera ulmifolia* (Turneraceae). *Funct. Ecol.* 17: 417-423.
- DEYRUP, M. 2003. An updated list of Florida ants (Hymenoptera: Formicidae). *Florida Entomol.* 86: 43-48.
- DEYRUP, M., CARLIN, N., TRAGER, J., AND UMPHREY, G. 1988. A Review of the Ants of the Florida Keys. *Florida Entomol.* 71: 163-176.
- DIAZ-CASTELAZO, C., RICO-GRAY, V., OLIVEIRA, P. S., AND CUAUTLE, M. 2004. Extrafloral nectary-mediated ant-plant interactions in the coastal vegetation of Veracruz, Mexico: Richness, occurrence, seasonality, and ant foraging patterns. *Ecoscience* 11: 472-481.
- DIAZ-CASTELAZO, C., RICO-GRAY, V., ORTEGA, F., AND ANGELES, G. 2005. Morphological and secretory characterization of extrafloral nectaries in plants of coastal Veracruz, Mexico. *Ann. Bot., London* 96: 1175-1189.
- DOAK, P., WAGNER, D., AND WATSON, A. 2007. Variable extrafloral nectary expression and its consequences in quaking aspen. *Canadian J. Botany* 85: 1-9.
- FARJI-BRENER, A., CORLEY, J. C., AND BETTINELLI, J. 2002. The effects of fire on ant communities in north-western Patagonia: the importance of habitat structure and regional context. *Divers. Distrib.* 8: 235-243.
- FIALA, B., AND LINSENMAIR, K. E. 1995. Distribution and abundance of plants with extrafloral nectaries in the woody flora of a lowland primary forest in Malaysia. *Biodivers. Conserv.* 4: 165-182.
- FIALA, B., AND MASCHWITZ, U. 1991. Extrafloral nectaries in the genus *Macaranga* (Euphorbiaceae) in Malaysia: comparative studies of their possible significance as predispositions for myrmecophytes. *Biol. J. Linn. Soc.* 44: 287-305.

- GOITIA, W., AND JAFFE, K. 2009. Ant-plant associations in different forests in Venezuela. *Neotrop. Entomol.* 38: 7-31.
- HEADS, P. A. 1986. Bracken, ants and extrafloral nectaries: IV. Do wood ants (*Formica lugubris*) protect the plant against insect herbivores? *J. Anim. Ecol.* 55: 795-809.
- HEADS, P. A., AND LAWTON, J. H. 1984. Bracken, ants and extrafloral nectaries. II. The effect of ants on the insect herbivores of bracken. *J. Anim. Ecol.* 53: 1015-1031.
- HEIL, M., AND MCKEY, D. 2003. Protective ant-plant interactions as model systems in ecological evolutionary research. *Annu. Rev. Ecol. Syst.* 34: 425-453.
- HEIL, M. 2008. Indirect defence via tritrophic interactions. *New Phytol.* 178:41-61.
- HENRY, P. W. T. 1974. The Pine Forests of the Bahamas. British Foreign and Commonwealth Office Land Resource Study. No. 16.
- HOFFMAN, B. D. 2003. Responses of ant communities to experimental fire regimes on rangelands in the Victoria river district of the Northern Territory. *Austral. Ecol.* 28: 182-195.
- HOLLAND, J. N., CHAMBERLAIN, S. A., AND HORN, K. C. 2009. Optimal defence theory predicts investment in extrafloral nectar resources in an ant-plant mutualism. *J. Ecol.* 97: 89-96.
- INOUE, D. W., AND TAYLOR, O. R. 1979. A temperate region plant-ant-seed predator system: consequences of extrafloral nectar secretion by *Helianthella quinquerervis*. *Ecology* 60: 1-8.
- IPSER, R. M., BRINKMAN, M. A., GARDNER, W. A., AND PEELER, H. B. 2004. A survey of ground-dwelling ants (Hymenoptera: Formicidae) in Georgia. *Florida Entomol.* 87: 253-260.
- JANZEN, D. H. 1966. Coevolution between ants and acacias in Central America. *Evolution* 20: 249-275.
- JANZEN, D. H. 1967. Interaction of the bull's horn acacia (*Acacia cornigera*) with an ant inhabitant (*Pseudomyrmex ferruginea*) in East Mexico. *Kansas Univ. Sci. Bull.* 47: 315-558.
- KASPARI, M., AND MAJER, J. D. 2000. Using Ants to Monitor Environmental Change, pp. 89-98 *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz [eds.], *Ants: Standard Methods for Measuring and Monitoring Biodiversity*. Smithsonian Institution Press, Washington.
- KEELER, K. H. 1979. Distribution of plants with extrafloral nectaries and ants at two elevations in Jamaica. *Biotropica* 11: 152-154.
- KEELER, K. H. 1981. Function of *Mentzelia nuda* (Loasaceae) postfloral nectaries in seed defense. *American J. Bot.* 68: 295-299.
- KEELER, K. H. 1985. Extrafloral nectaries on plants in communities without ants: Hawaii. *Oikos* 44: 407-414.
- KEELER, K. H. 2008. World List of Angiosperms with Extrafloral Nectaries. <http://www.biosci.unl.edu/Emeriti/keeler/extrafloral/Cover.htm>
- KERSCH, M. F., AND FONSECA, C. R. 2005. Abiotic factors and the conditional outcome of an ant-plant mutualism. *Ecology* 86: 2117-2126.
- KING, J., AND PORTER, S. 2005. Evaluation of sampling methods and species richness estimators for ants in upland ecosystems in Florida. *Environ. Entomol.* 34: 1566-1578.
- KOPTUR, S. 1984. Experimental evidence for defense of *Inga* (Mimosoideae) saplings by ants. *Ecology* 65: 1787-1793.
- KOPTUR, S. 1985. Alternative defenses against herbivores in *Inga* (Fabaceae: Mimosoideae) over an elevational gradient. *Ecology* 66: 1639-1650.
- KOPTUR, S. 1992a. Interactions between Insects and Plants Mediated by Extrafloral Nectaries, pp. 85-132 *In* E. Bernays [ed.], *CRC series on Insect/Plant Interactions*. Volume 4.
- KOPTUR, S. 1992b. Plants with extrafloral nectaries and ants in Everglades habitats. *Florida Entomol.* 75:38-50.
- KOPTUR, S. 1994. Floral and extrafloral nectars of neotropical *Inga* trees: a comparison of their constituents and composition. *Biotropica* 26:276-284.
- KOPTUR, S. 2005. Nectar as fuel for plant protectors, pp. 75-108, Ch. 3, *In* F. L. Wäckers, P. C. J. van Rijn, and J. Bruin [eds.], *Plant-provided Food for Carnivorous Insects: A Protective Mutualism and its Applications*. Cambridge University Press, Cambridge.
- KOPTUR, S., AND LAWTON, J. H. 1988. Interactions among vetches bearing extrafloral nectaries, their biotic protective agents, and herbivores. *Ecology* 69: 278-283.
- KOST, C., AND HEIL, M. 2005. Increased availability of extrafloral nectar reduces herbivory in Lima bean plants (*Phaseolus lunatus*, Fabaceae). *Basic Appl. Ecol.* 6: 237-248.
- KUO, J. AND PATE, J. S. 1985. The extrafloral nectaries of cowpea [*Vigna unguiculata* (L.) Walp.] I. Morphology, anatomy and fine structure. *Planta* 166: 15-27
- LIU, H., TRUSTY, J., OVIEDO, R., ANDERBERG, A., AND FRANCISCO-ORTEGA, J. 2004. Molecular phylogenetics of the Caribbean genera *Rhodogeron* and *Sachsia* (Asteraceae). *Int. J. Plant Sci.* 165: 209-217.
- LOOPE, L., DUEVER, M., HERNDON, A., SNYDER, J., AND JANSEN, D. 1994. Hurricane impact on uplands and freshwater swamp forest. *Bioscience* 44: 238-246.
- MACHADO, S. R., MORELLATO, L. P. C., SAJO, M. G., AND OLIVEIRA, P. S. 2008. Morphological patterns of extrafloral nectaries in woody plant species of the Brazilian cerrado. *Plant Biol.* 10: 660-673.
- MATHEWS, C. R., BOTTRELL, D. G., AND BROWN, M. W. 2009. Extrafloral nectaries alter arthropod community structure and mediate peach (*Prunus persica*) plant defense. *Ecol. Appl.* 19: 722-730.
- MEXZON, R. G., AND CHINCHILLA, C. M. 1998. Plant species attractive to beneficial entomofauna in oil palm (*Elaeis guineensis* Jacq.) plantations in Costa Rica. *ASD Oil Palm Papers* No. 19, 1-22.
- MIZELL, R. F. 2004. Many plants have extrafloral nectaries helpful to beneficials. *USDA ARS* <http://edis.ifas.ufl.edu/IN175>
- MODY, K., AND LINSENMAIR, K. E. 2004. Plant-attracted ants affect arthropod community structure but not necessarily herbivory. *Ecol. Entomol.* 29: 217-225.
- MONDOR, E. B., TREMBLAY, M. N., AND MESSING, R. H. 2006. Extrafloral nectary phenotypic plasticity is damage- and resource-dependent in *Vicia faba*. *Biological Lett.* 2: 583-585.
- MORRISON, L. W. 2002. Island biogeography and metapopulation dynamics of Bahamian ants. *J. Biogeography* 29: 387-394.
- MORRISON, L. W. 2003. Plant species persistence and turnover on small Bahamian islands. *Oecologia* 136: 51.
- MORRISON, L. W., AND SPILLER, D. A. 2008. Patterns and processes in insular floras affected by hurricanes. *J. Biogeography* 35: 1701-1710.

- NESS, J. H. 2006. A mutualism's indirect costs: the most aggressive plant bodyguards also deter pollinators. *Oikos* 113: 506-514.
- NUESSLY, G. S., HENTZ, M. G., BEIRIGER, R., AND SCULLY, B. T. 2004. Insects associated with faba bean, *Vicia faba* (Fabales: Fabaceae), in southern Florida. *Florida Entomol.* 87: 204-211.
- O'BRIEN, J. J., STAHALA, C., MORI, G. P., CALLAHAM, JR., M. A., AND BERGH, C. M. 2006. Effects of prescribed fire on conditions inside a Cuban parrot (*Amazona leucocephala*) surrogate nesting cavity on great Abaco, Bahamas. *Wilson J. Ornithol.* 118: 508-512.
- O'DOWD, D. J., AND CATCHPOLE, E. A. 1983. Ants and extrafloral nectaries: No evidence for plant protection in *Helichrysum* spp.-ant interactions. *Oecologia* 59: 191-200.
- O'DOWD, D. J., AND GILL, A. M. 1984. Predator satiation and site alteration following fire: mass reproduction of alpine ash (*Eucalyptus delegatensis*) in southeastern Australia. *Ecology* 65: 1052-1066.
- OLIVER, T. H., COOK, J. M., AND LEATHER, S. R. 2007. When are ant-attractant devices a worthwhile investment? *Vicia faba* extrafloral nectaries and *Lasius niger* ants. *Popul. Ecol.* 49: 265-273.
- OLIVEIRA, P. S., AND FREITAS, A. V. L. 2004. Ant-Plant-Herbivore Interactions in the Neotropical Cerrado Savanna. *Naturwissenschaften* 91: 557-570.
- PARR, C. L., BOND, W. L., AND ROBERTSON, H. G. 2002. A preliminary study of the effect of fire on ants (Formicidae) in a South African savanna. *African Entomol.* 10: 101-111.
- PARR, C. L., ROBERTSON, H. G., BIGGS, H. C., AND CHOWN, S. L. 2004. Response of African savanna ants to long-term fire regimes. *J. Appl. Ecol.* 41: 630-642.
- PASCAL, L. M., MOTTE-FLORAC, E. F., AND MCKEY, D. B. 2000. Secretory structure on the leaf rachis of Caesapineae and Mimosoideae (Leguminosae): Implications for the evolution of nectary glands. *American J. Bot.* 87: 327-338.
- PATE, J. S., PEOPLES, M. B., STORER, P. J., AND ATKINS, C. A. 1985. The extrafloral nectaries of cowpea (*Vigna unguiculata* (L.) Walp.): II. Nectar composition, origin of nectar solutes and nectar functioning. *Planta* 166: 28-38.
- PATTERSON, J., AND STEVENSON, G. 1977. native Trees of the Bahamas. The Bahamas National Trust. Hope Town, Abaco, Bahamas.
- PEMBERTON, R. W. 1990. The occurrence of extrafloral nectaries in Korean plants. *Korean J. Ecol.* 13(4): 251-266.
- PEMBERTON, R. W., AND LEE, J.-H. 1996. The influence of extrafloral nectaries on parasitism of an insect herbivore. *American J. Bot.* 83: 1187-1194.
- PEMBERTON, R. W. 1998. The occurrence and abundance of plants with extrafloral nectaries, the basis for anti-herbivore defensive mutualisms, along a latitudinal gradient in east Asia. *J. Biogeography* 25: 661-668.
- RASHBROOK, V. K., COMPTON, S. G., AND LAWTON, J. H. 1993. Ant-herbivore interactions: reasons for the absence of benefit to a fern with foliar nectaries. *Ecology* 73(6): 2167-2174.
- RATCHFORD, J. S., WITTMAN, S. E., JULES, E. S., ELLISON, A. M., GOTELLI, N. J., AND SANDERS, N. J. 2005. The effects of fire, local environment and time on ant assemblages in fens and forests. *Divers. Distrib.* 11: 487-497.
- RICO-GRAY, V., AND OLIVEIRA, P. S. 2007. The Ecology and Evolution of Ant-Plant Interactions. University of Chicago Press, Chicago.
- ROBERTSON, W. B. 1955. An Analysis of the Breeding Bird Populations of Tropical Florida in Relation to the Vegetation. Dissertation. University of Illinois.
- ROGERS, C. E. 1985. Extrafloral nectar: entomological implications. *Bull. Entomol. Soc. America* 31: 15-20.
- SANDERS, N. J. 2004. Immediate effects of fire on the invasive Argentine ant, *Linepithema humile*. *Southwest Nat.* 49: 246-250.
- SEALEY, N. E. 1985. Bahamian Landscapes, An Introduction to the Geography of the Bahamas. Collins Caribbean, London.
- SMILEY, J. T. 1985. *Heliconius* caterpillar mortality during establishment on plants with and without attending ants. *Ecology* 66(3): 845-849.
- SMITH, I. K., AND VANKAT, J. L. 1992. Dry evergreen forest (coppice) communities of North Andros Island, Bahamas. *Bull. Torrey Bot. Club* 119: 181-191.
- SNYDER, J. R., HERNDON, A., AND ROBERTSON, W. B. 1990. South Florida rockland, pp. 230-277 *In* R. L. Myers and J. J. Ewel [eds.], *Ecosystems of Florida*. University of Central Florida Press, Orlando, Florida.
- SO, M. L. 2004. The occurrence of extrafloral nectaries in Hong Kong plants. *Bot. Bull. Acad. Sin.* 45: 237-245.
- SOLOMON, S. E., AND MIKHEYEV, A. S. 2005. The ant (Hymenoptera: Formicidae) fauna of Cocos Island, Costa Rica. *Florida Entomol.* 88:415-423.
- SOUSA E PAIVA, E. A., CASTANHEIRA DE MORAIS, H., MARY DOS SANTOS ISAIAS, R., SUCENA DA RICHIA, D. M., AND OLIVEIRA, P. E. 2001. Occurrence and structure of extrafloral nectaries in *Pterodon pubescens* Benth. and *P. polygalaeiflorus* Benth. *Pesq. Agropec. Bras., Brasilia* 36: 219-224.
- SPSS 2002. SPSS for Windows version 11.5. LEAD Technologies, Inc.
- SUZUKI, N., OGURA, K., AND KATAYAMA, N. 2004. Efficiency of herbivore exclusion by ants attracted to aphids on the vetch *Vicia angustifolia* L. (Leguminosae). *Ecol. Res.* 19: 275-282.
- TEMPEL, A. S. 1983. Bracken fern (*Pteridium aquilinum*) and nectar-feeding ants: a nonmutualistic interaction. *Ecology* 64: 1411-1422.
- TILMAN, D. 1978. Cherries, ants and tent caterpillars: timing of nectar production in relation to susceptibility to ant predation. *Ecology* 59: 6686-692.
- VALENZUELA-GONZALEZ, J., QUIROZ-ROBLEDO, L., AND MARTINEZ-TLAPA, D. L. 2008. Hormigas (Insecta: Hymenoptera: Formicidae), pp 107-121 *In* R. H. Manson, V. Hernandez-Ortiz, S. Gallina and K. Mehlreter [eds.], *Agroecosistemas Cafetaleros de Veracruz - Biodiversidad, Manejo, y Conservacion*. Instituto de Ecología, A.C., Xalapa.
- WETTERER, J. K., MILLER, S. E., WHEELER, D. E., OLSON, C. A., POLHEMUS, D. A., PITTS, M., ASHTON, I. W., HIMLER, A. G., YOSPIN, M. M., HELMS, K. R., HARKEN, E. L., GALLAHER, J., DUNNING, C. E., NELSON, M., LITSINGER, J., SOUTHERN, A., AND BURGESS, T. L. 1999. Ecological dominance by *Paratrechina longicornis* (Hymenoptera: Formicidae), an invasive tramp ant, in Biosphere 2. *Florida Entomol.* 82: 381-388.
- WETTERER, J. K., AND WETTERER, A. L. 2003. Ants (Hymenoptera: Formicidae) on non-native neotropical ant-acacias (Fabales: Fabaceae) in Florida. *Florida Entomol.* 86: 460-463.

- WHITNEY, K. D. 2004. Experimental evidence that both parties benefit in a facultative plant-spider mutualism. *Ecology* 85: 1642-1650.
- WICKERS, S. 1997. Etude de la secretion nectarifere d'une plante pionniere, *Inga thibaudiana*, en relation avec les fourmis. *Acta bot. Gallica* 144: 315-326.
- WOOLEY, S. C., DONALDSON, J. R., GUSSE, A. C., LINDROTH, R. L., AND STEVENS, M. T. 2007. Extrafloral nectaries in aspen (*Populus tremuloides*): heritable genetic variation and herbivore-induced expression. *Ann. Bot., London* 100: 1337-1346.