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PLANTS WITH EXTRAFLORAL NECTARIES AND ANTS IN EVERGLADES HABITATS

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ABSTRACT

The terrestrial vegetation of the inland areas of the Everglades is of three main types, occurring on oolite limestone substrate of progressively higher elevation: sawgrass prairie, or glade; pineland; and hardwood hammock. Nectar-drinking ant abundance was assessed using transects of honey baits, and is highest in pineland, and lowest in glade habitat. Recruitment of ants to baits is also highest in pineland. Out of 891 species of

vascular plants in Everglades National Park, 78 spp. (9%) in 29 families have extrafloral nectaries. The proportion of species with extrafloral nectaries was highest in pineland, as was the proportion of individuals with extrafloral nectaries. The pinelands, with the greatest nectar-drinking ant abundance, have the most plants with extrafloral nectaries. Eight ant species have been collected at honey baits, and four species are regular visitors to extrafloral nectaries of plants. Nectary-visiting ants are potential protectors of plants against herbivores.

RESUMEN

Los Everglades estan integrados por tres tipos principales de vegetación terrestre, los cuales ocurren en roca caliza del oolito con una elevación progresiva: pradera, bosque de pinos y bosque maderable. Se evaluó la abundancia de las hormigas que se alimentan de nectar, usando cebos con miel de abejas y fué mas alta en el bosque de pinos y mas baja en la pradera. La captura de otras hormigas en cebos fué también mas alta en el bosque de pinos. De las 891 especies de plantas vasculares que existen en el parque nacional de los Everglades, 78 especies (8%) en 29 familias tienen nectar extrafloral. La proporción de especies con nectar extrafloral fue mayor en bosque de pinos (27%), que en bosque maderable (22%) y que en la pradera (12%), pero la proporción de individuos con nectar extrafloral fue mayor (34%) en bosque de pinos que en bosque maderable (23%) o en la pradera (2%). Los bosques de pino, con la mayor abundancia de hormigas consumidoras de nectar, tienen el mayor numero de plantas con nectar extrafloral. Ocho especies de hormigas se han colectado en los cebos con miel de abejas y cuatro especies son visitantes frecuentes de los nectares extraflorales. Las hormigas visitantes de los nectares extraflorales protegen potencialmente la planta contra el ataque de herbivoros.

Extrafloral nectaries are plant secretory structures of diverse morphology and anatomy (Elias 1983). They are located outside of flowers, and therefore do not usually involve pollination. They are visited by a wide variety of animals for energy and nutrition, and the associated effects on the plants range from beneficial (e.g., patrolling of plant surfaces and disturbance of herbivores; enhanced predation and parasitism of plant feeders) to harmful (e.g., attraction of herbivorous insect adults who oviposit on the plant), depending on the ecological context (Bentley 1977, Beattie 1984, Buckley 1982, Koptur 1992).

Extrafloral nectaries can be found on plants in both the tropics and temperate zones, although they are more common in tropical areas. Biologists have surveyed various habitats in diverse geographic locations and have determined the proportion of plants that bear extrafloral nectaries (Table 1); some have sought to correlate abundance of plants bearing extrafloral nectaries with the abundance or activity of ants at different sites (Bentley 1976, Keeler 1979a, Koptur 1985, Koptur 1989, Koptur et al 1977), and in general, have found fewer nectary-bearing individuals in areas with few or no ants.

This study is a contribution to this ongoing world survey. I examine the diversity of plants with extrafloral nectaries in subtropical south Florida, and their distribution in upland habitats of Everglades National Park. The unique combination of temperate and tropical plants and animals has resulted in the designation of the Everglades as an International Biosphere Preserve. The working hypothesis is that there will be an intermediate proportion of the flora bearing extrafloral nectaries (more than temperate sites, and less than tropical sites), and an intermediate diversity of plant species with nectaries and ants that occur in the same habitats.

The upland terrestrial vegetation of the Everglades is of three main types: wet prairie, pineland, and hardwood hammock. The seasonally inundated sawgrass prairie, or glades is the lowest elevation habitat, has a substrate of marl over limestone rock,

TABLE 1. COVER OF PLANTS WITH EXTRAFLORAL NECTARIES IN VARIOUS LOCATIONS.

% mean cover	Location	Vegetation types/% cover	Reference
2-34%	Everglades, Florida, USA	sawgrass prairie 2% rockledge pinelands 34% hardwood hammock 23%	Koptur 1989 (data updated)
0%	N. California, USA	native grassland 0% riparian forest 0% deciduous forest 0% chapparal 0%	Keeler 1980a
0-14.2%	Nebraska, USA	deciduous forest 1.8% riparian forest 1.3% tallgrass prairie 0% sandhills prairie 8.3%	Keeler 1980b
0-27.8%	S. California, USA	desert bush scrub 0.1-6.6% desert wash 23.9-27.8% sand dunes 0-1.4% yucca-agave 3.7%	Pemberton 1988
7.5-55%	Korea	deciduous forest	Pemberton 1990
0-28%	Jamaica	forested second growth (0 m) 28% same-at 1310 m 0%	Keeler 1979a
7.6-20.3%	SE Brazil	cerrado (woody spp. only)	Oliveira & Leitão-Filho 1987
21.6-31.2%	SW Brazil	cerrado (woody spp.)	"", Oliveira & Oliveira-Filho 1991
17.6-53.3%	Amazonian Brazil	terra firme forest 19.1% successional forest 42.6% buritirana 29.7% shrub canga 50%	Morellato & Oliveira 1992
10-80%	Costa Rica	dryforest hillside 40-80% riparian forest 10-40%	Bentley 1976
0-22%	Costa Rica	rain forest (0 m) 1-8% cloud forest (1500 m) 3-22% oak forest (3000 m) 0-3%	Koptur et al. 1977

and is comprised mostly of herbaceous perennials and annuals, with scattered shrubs (Fig. 1). The pineland is a subclimax community maintained by fire, on limestone rock a few inches higher in elevation, consisting of an overstory of Dade county slash pine (*Pinus elliottii* Engelm. var. *densa* Little & Dorman) and an understory of herbs, vines, and shrubs (Fig. 2). Fire cleans out the developing hardwood understory every five or so years, permitting the pines to remain the dominant feature. Without fire, the hardwoods grow larger and eventually a hardwood forest, or hammock, is formed (Fig. 3). These habitats are intertwined into a mosaic due to small differences in topography, fire history, and water flow.

METHODS

Field observations and experiments were conducted in Everglades National Park from 1987 - 1991 in Long Pine Key, in the vicinity of Redd Hammock. Extrafloral



Fig. 1. Sawgrass prairie (glade) habitat in Everglades National Park.

nectaries on plants were detected by visual inspection, sometimes aided by hand-lens and dissecting microscope. The presence of ants or sooty mold gave evidence of nectar secretion (if ant-tended Homoptera were not present). Certain species did not have obvious nectaries, but close examination, prompted by reports in the literature that their families or genera possessed nectaries, often revealed tiny nectaries.

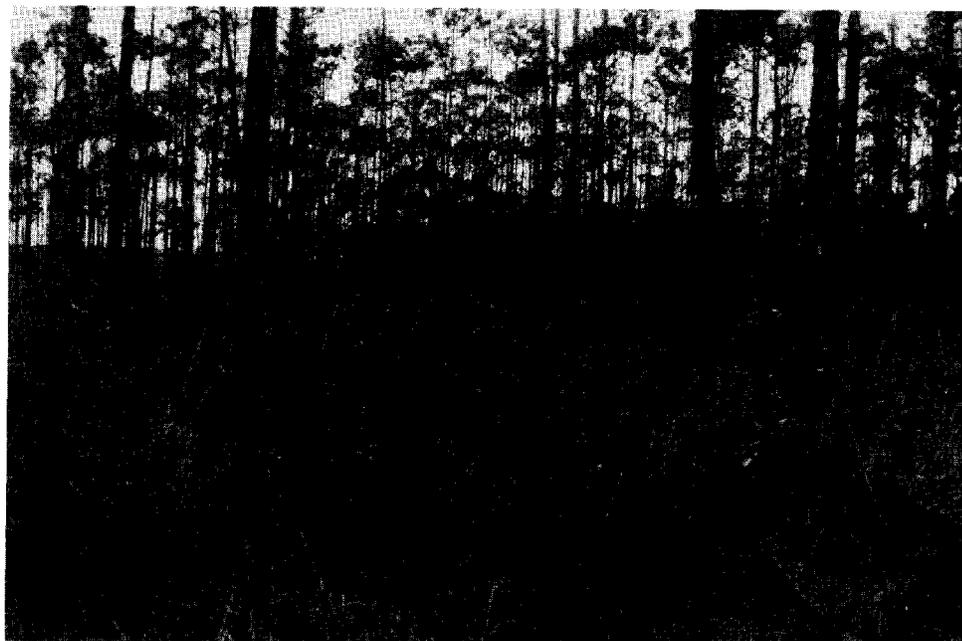


Fig. 2. Pineland habitat in Everglades National Park.

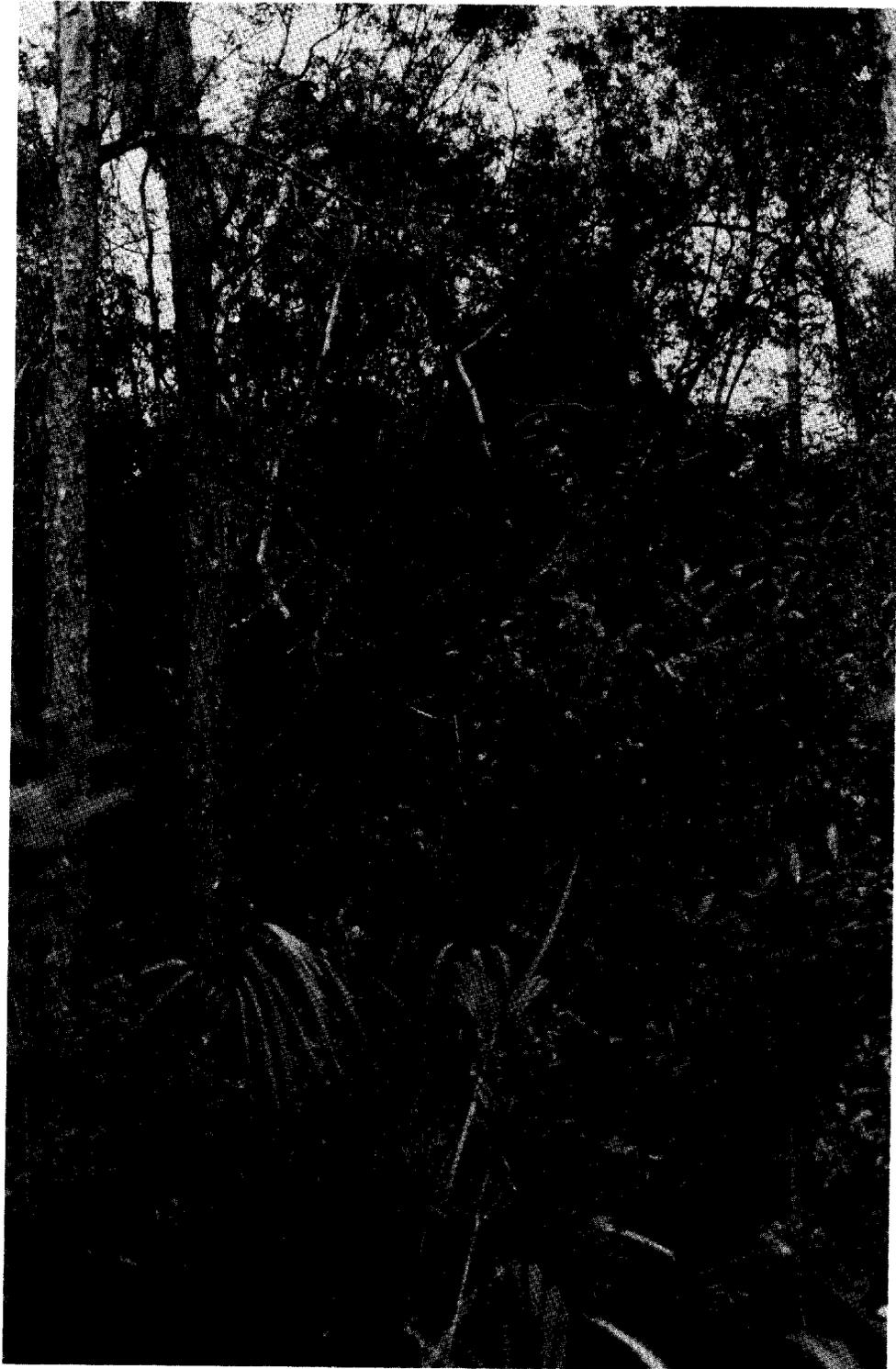


Fig. 3. Hammock habitat in Everglades National Park.

Cover of plants with extrafloral nectaries was determined using three 20 m transects in each of the three habitats. These nine transects were done during the early dry season, when the sawgrass prairie is not covered with water, and so reflect only the plants present during late November.

Ant activity was measured using lines of honey baits at four times during the dry season: November, February, March, and April. Each line consisted of 20 baits spaced at 1 m intervals, and was monitored every 5 minutes for 1 hour. The numbers and types of ants attracted to the baits were recorded at each observation. A bait was considered "discovered" if any ants at all were present at any time, and to have experienced "recruitment" if the number of ants increased to greater than five. Ant voucher specimens were determined by Dr. Mark Deyrup of Archbold Biological Station.

RESULTS

Of the 891 species of vascular plants recorded for Everglades National Park (Avery & Loope 1983), 78 species in 29 families (8.8 %) have been observed to possess extrafloral nectaries (Table 2). Common families with extrafloral nectaries include the legumes (Fabaceae), from foliar nectaries on trees such as *Lysiloma bahamensis* Benth. and

TABLE 2. TERRESTRIAL PLANT SPECIES WITH EXTRAFLORAL NECTARIES IN EVERGLADES NATIONAL PARK. E* = EXOTIC SPECIES. POSITION OF NECTARIES IS INDICATED BY NUMBERS: 1 = ON LEAF, 2 = ON PETIOLE, 3 = ON STIPULES AND/OR STIPELS, 4 = ON STEMS, 5 = ON PEDICELS, PEDUNCLES, OR STEMS OF INFLORESCENCE, 6 = ON PETALS OR SEPALS, 7 = ON BRACTS, 8 = ON FRUIT, CAPSULE, OR POD, 9 = ON OVARY (POST-FLORAL), 10 = ABORTED FLOWERS OR BUD SCARS.

Ferns:

PTERIDACEAE

Pteridium aquilinum (L.) Kuhn var. *caudatum* (L.) Sadebeck (1)

Monocots:

BROMELIACEAE

Tillandsia balbisiana Schult. (5)

DIOSCOREACEAE

E* *Dioscorea bulbifera* L. (1)

LILIACEAE

Smilax auriculata Walt. (1)

Smilax bona-nox L. (1)

Smilax havanensis Jacq. (1)

Smilax laurifolia L. (1)

ORCHIDACEAE

Encyclia boothiana (Lindl.) Dressler var. *erythronioides* (Small) Luer (5)

E. cochleata (L.) Dressler var. *triandra* (Ames) Dressler (5)

E. tampensis (Lindl.) Small (5)

Epidendrum nocturnum Jacq. (5)

E. rigidum Jacq. (5)

Oncidium ensatum Lindl. (*O. floridanum*) (4,5)

O. altissimum (Jacq.) Sw. (*O. luridum*) (4,5)

Vanilla barbellata Reichb. f. (5)

V. phaeantha Reichb. f. (5)

POACEAE

E* *Eragrostis barrelieri* Daveau (5)

Eragrostis ciliaris (L.) R. Br. (5)

E. elliottii S. Wats. (5)

TABLE 2. (CONTINUED).

Dicots:

ANNONACEAE

Annona glabra L. (8)

CAPRIFOLIACEAE

Sambucus canadensis L. (*S. simpsonii*) (1)

CHRYSOBALANACEAE

Chrysobalanus icaco L. (1)

COMBRETACEAE

Conocarpus erectus L. (2)E* *Terminalia catappa* L. (2)

CONVOLVULACEAE

Ipomoea alba L. (2)*I. hederifolia* L. (2)*I. indica* (Burm.) Merrill (*I. acuminata*) (2)*I. trichocarpa* Ell. (2)*I. triloba* L. (2)

EBENACEAE

Diospyros virginiana L. (1)

EUPHORBIACEAE

Cnidocolus stimulosus (Michx.) Engelm. & Gray (1,2)*Croton arenicola* Small (*C. glandulosus*) (1)*C. linearis* Jacq. (1)*Hippomane mancinella* L. (1)*Manihot esculenta* Crantz (1)

FABACEAE

Acacia farnesiana (L.) Willd. (1)*A. pinetorum* Hermann (1)*Albizia lebeck* (L.) Benth. (1)*Canavalia brasiliensis* Mort ex. Benth. (1)*C. rosea* (Sw.) DC. (1)*Cassia aspera* Muhl. ex Ell. (2)*C. chapmanii* Isely (2)*C. deeringiana* (Small & Penn.) Macbr. (2)E* *C. fistula* L. (2)*C. ligustrina* L. (2)*C. obtusifolia* L. (2)E* *Delonix regia* (Boj. ex Hook.) Raf. (2)*Erythrina herbacea* L. (3)E* *Leucaena leucocephala* (Lam.) de Wit (2)*Lysiloma latisiliquum* (L.) Benth. (1)*Pithecellobium guadalupense* (Pers.) Chapm. (1)*P. unguis-cati* (L.) Benth. (1)*Vigna luteola* (Jacq.) Benth. (5)

GOODENIACEAE

Scaevola plumieri (L.) Vahl (1)

MALVACEAE

Gossypium hirsutum L. (1)E* *Hibiscus rosa-sinensis* L. (1)E* *Thespesia populnea* (L.) Soland. ex Correa (1)E* *Urena lobata* L. (1)

MELIACEAE

Suietenia mahogani (L.) Jacq. (1)

MORACEAE

Ficus aurea Nutt. (8)

MYRSINACEAE

Myrsine floridana A. DC. (1)

PASSIFLORACEAE

- Passiflora pallens* Poepp. ex Mast. (1)
P. sexflora Juss. (1)
P. suberosa L. (1,2)

RHAMNACEAE

- Colubrina arborescens* (Mill.) Sarg. (1)
C. cubensis (Jacq.) Brongn. var. *floridana* M.C. Johnst. (1)
C. elliptica (Sw.) Briz. & Stern (= *C. reclinata*) (1)

ROSACEAE

- Prunus myrtifolia* (L.) Urb. (1)

RUBIACEAE

- Hamelia patens* Jacq. (9)
Morinda royoc L. (9)

RUTACEAE

- Zanthoxylum fagara* (L.) Sarg. (1)

STERCULIACEAE

- Ayenia euphasiifolia* Greiseb. (1)

TILIACEAE

- E* *Triumfetta semitriloba* Jacq. (1)

TURNERACEAE

- Turnera ulmifolia* L. var. *ulmifolia* (2)

VERBENACEAE

- Avicennia germinans* (L.) L. (2)
Citharexylum fruticosum L. (1)

- E* *Clerodendrum speciosissimum* Van Geert ex C. Morr. (1)

VITACEAE

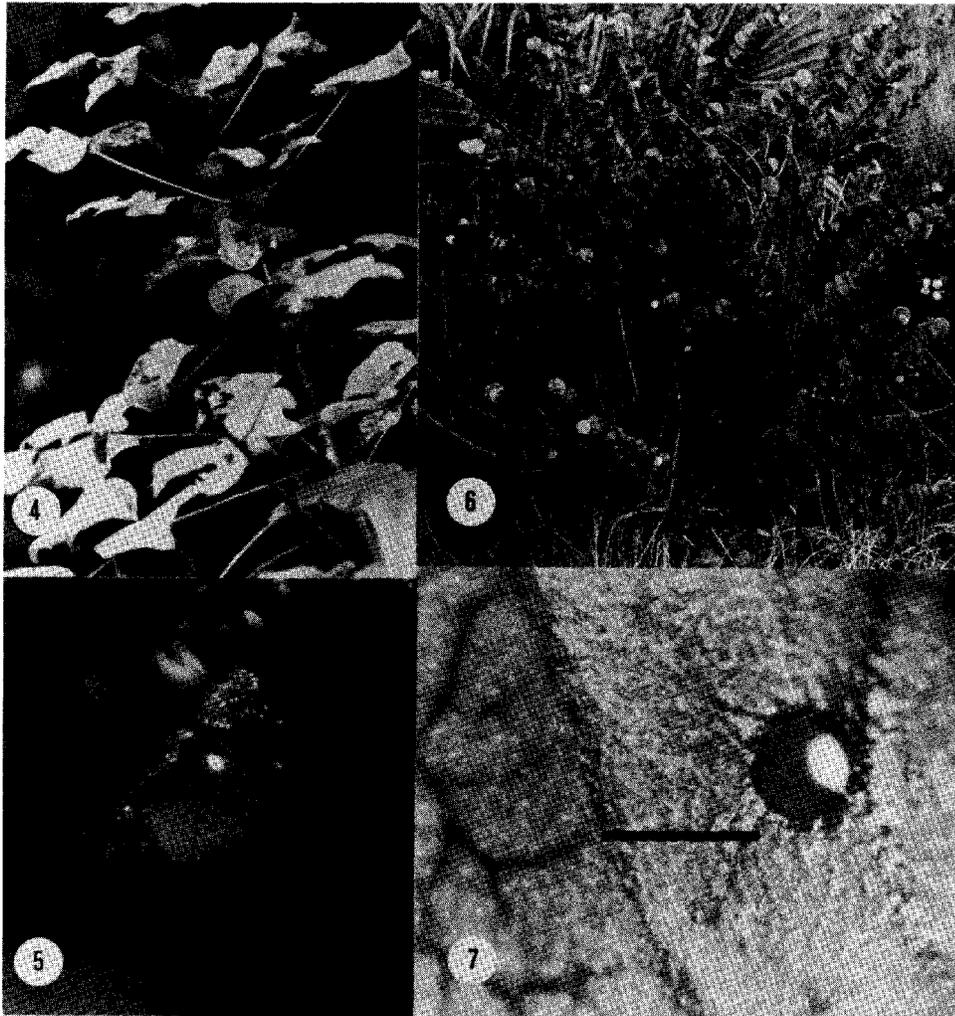
- Cissus sicyoides* L. (1)

treelets like *Erythrina herbacea* L. (Figs. 4 & 5) to herbs such as the rockledge-dwelling *Cassia deeringiana* (Small & Penn.) Macbr.; the orchids (Orchidaceae) with nectaries in the inflorescence; the mallows (Malvaceae) with foliar nectaries on the lower abaxial surface of the lamina; and the passionflowers (Passifloraceae) with elevated nectaries on leaf bases and petioles (Fig. 8). Prompted by observations by Kathy Keeler, I have observed formless nectaries on the young inflorescences of *Tillandsia balbisiana* Schult. (Bromeliaceae) (Fig. 9). And prompted by a report of nectaries in *Rapanea* (Myrsinaceae) (Oliveira & Leitão-Filho 1987), Bob Pemberton and I observed foliar nectaries in *Myrsine floridana* A.DC. for the first time (Figs. 10-12).

Transects revealed the greatest plant species diversity in the pinelands, followed by glade, and then hammocks (Table 3). The pinelands had the highest proportion of species with extrafloral nectaries (27%, vs. 22% in hammocks and 12% in glade). This difference is even more striking when we compare cover of plants with nectaries (the proportion of individuals with nectaries): 34% of the plants encountered in pinelands were species that bear nectaries; 23% in hammocks; and only 2.5% in glade.

The discovery of honey baits by ants (and presumably, ant activity and/or abundance) was greatest in pineland (a mean of 9.8 baits out of 20 discovered in one hour), intermediate in hardwood hammock (a mean of 4.2 baits discovered in one hour) and lowest in the glade (a mean of 1 bait out of 20 discovered in one hour) (Table 4). Recruitment of ants to baits is also highest in pineland (a mean of 3.6 baits recruited to, versus a mean of 2 in hammock, and none whatsoever in glade) (Table 4).

Of the 50 species (40 native, 10 exotic) of ants recorded from Everglades National Park (Alan Herndon and Mark Deyrup, personal communication), I have found 8 species visiting honey baits at my study sites (Table 5). Four of these species are regular visitors to extrafloral nectaries of various plants.

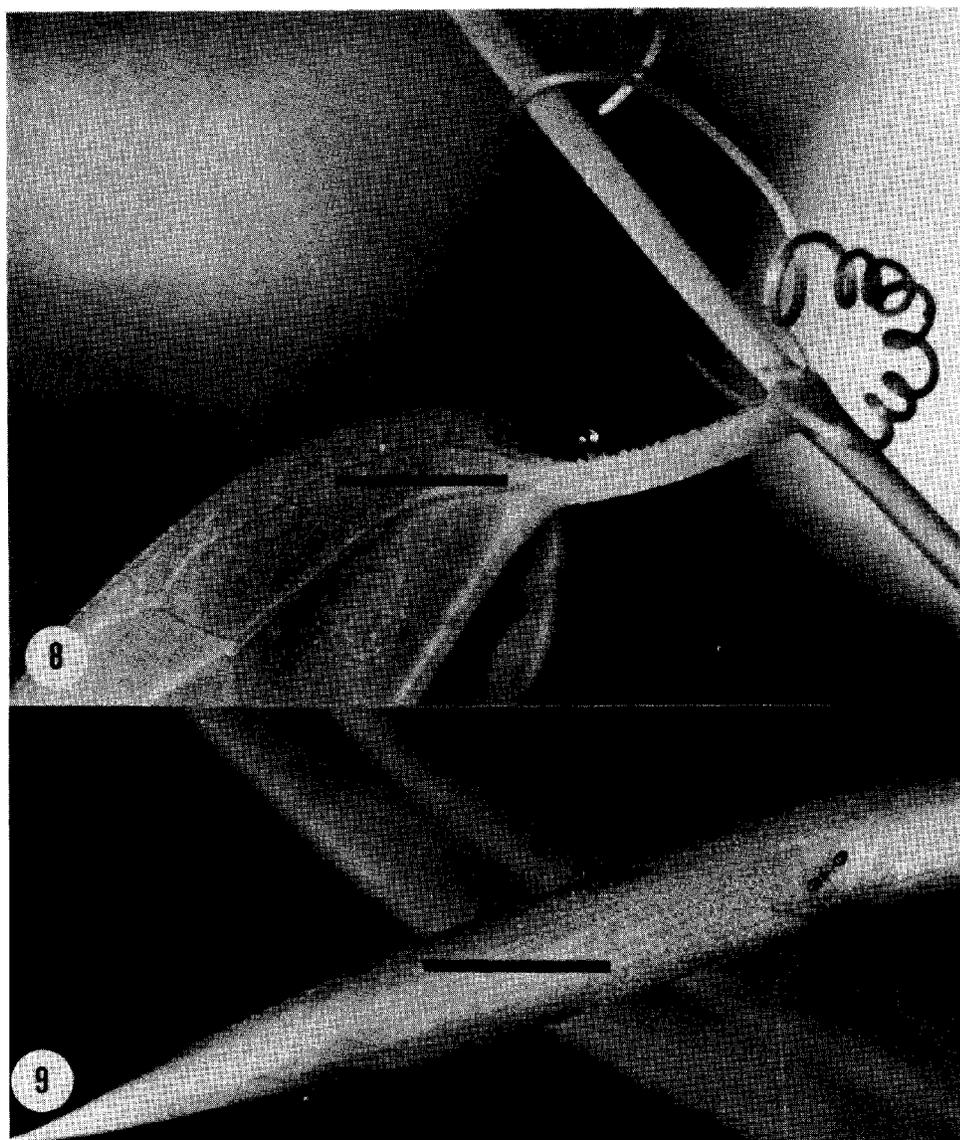


Figs. 4-7. Some Everglades plants with extrafloral nectaries. 4. Habit of coral bean, *Erythrina herbacea* (Fabaceae), a small tree that bears nectaries on the stipels of its trifoliate leaves. 5. Nectar secreted from one of a pair of stipel nectaries on young leaves of *E. herbacea*. Bar scale = 0.5 mm. 6. Habit of cocoplum, *Chrysobalanus icaco* L. (Chrysobalanaceae). 7. Flattened nectary with nectar on abaxial leaf surface near base on young leaf of *C. icaco*. Bar scale = 1 mm.

DISCUSSION

The pineland has the greatest ant activity and recruitment, and therefore, the greatest potential for ant protection of plants with extrafloral nectaries. The pineland also has the greatest number of plants with extrafloral nectaries. Exclusion experiments performed on a common tree of pinelands and hammocks, the wild tamarind (*Lysiloma bahamensis*), have demonstrated that the presence of ants reduces damage to leaves (Koptur unpublished results). The role of ants and other beneficial insects visiting nectaries of other pineland species awaits elucidation.

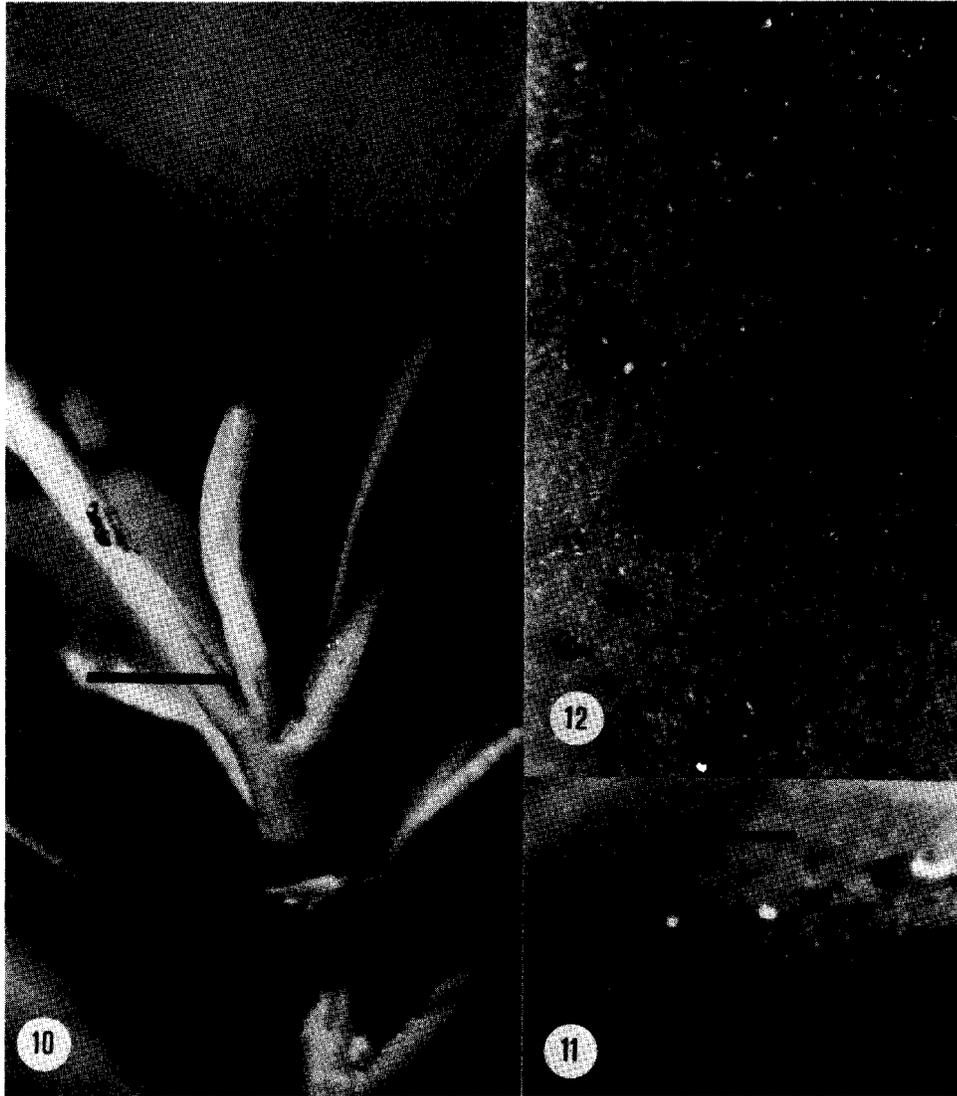
The proportion of species in a flora bearing extrafloral nectaries has been calculated for a number of habitats around the world. These values range from less than 5% in southern California (Pemberton 1988), Hawaii (Keeler 1985), Korea (Pemberton 1990)



Figs. 8-9. Some Everglades plants with extrafloral nectaries. 8. Nectar droplet on elevated nectary of *Passiflora suberosa* L. (Passifloraceae). Bar scale = 1 cm. 9. Ants visiting formless nectaries on young inflorescences of *Tillandsia balbisiana* (Bromeliaceae). Bar scale = 1 cm.

and Nebraska (Keeler 1979b) to more than 15% in various habitats of Brazil (Oliveira & Leitão-Filho 1987, Oliveira & Oliveira-Filho 1991). The proportion of the Everglades flora with extrafloral nectaries is intermediate, with a value of 9% (78 of 891 spp.). This proportion may increase slightly with more field observations.

The cover of plants with extrafloral nectaries has been documented in a variety of tropical and temperate locations (Table 4) and ranges from 0% in northern California, Nebraska, and high elevation tropical sites to more than 50% in Costa Rica and Amazonian Brazil. In general, there are more individuals with extrafloral nectaries in tropical habitats than temperate habitats. Upland habitats of south Florida have from 2% to



Figs. 10-12. Some Everglades plants with extrafloral nectaries. 10. Ant visiting formless nectaries of *Myrsine floridana* located on abaxial leaf surfaces at leaf base on either side of the midrib. Bar scale = 1 cm. 11. Underside of leaf edge of *M. floridana* with nectar droplets. Bar scale = 1 mm. 12. Leaf surface with formless nectaries of *M. floridana*. Bar scale = 0.5 mm.

34% cover of extrafloral nectary-bearing plants, intermediate between temperate and tropical extremes.

Upland habitats of south Florida are not the only ones in which ants exist, and preliminary observations have revealed that plants with extrafloral nectaries are also found in inundated freshwater and saltwater habitats. (These species are included in Table 2.) Future work will compare other habitats in south Florida to upland habitats of the Everglades, and investigate the potential ecological role of extrafloral nectaries in various native plant species.

TABLE 3. PLANTS WITH EXTRAFLORAL NECTARIES IN THREE HABITATS.

Habitat	Number of species encountered	Proportion (No.) spp. nectaries	Number of individuals encountered	Proportion indivs. with nectaries
glade	26	12% (3)	242	2.5% (6)
pineland	3	27% (9)	353	34% (121)
hammock	23	22% (5)	197	23% (46)

TABLE 4. ANT ACTIVITY AT BAITS IN THREE HABITATS IN EVERGLADES NATIONAL PARK. NUMBERS IN THE TABLE ARE (D) THE NUMBERS OF BAITS OUT OF 20 THAT WERE DISCOVERED BY ANTS IN THE HOUR AND (R) THE NUMBERS OF BAITS TO WHICH RECRUITMENT TOOK PLACE.

Habitat	14 Nov 87		13 Feb 88		28 Mar 88		04 Apr 88		mean	
	D	R	D	R	D	R	D	R	D	R
glade	0	0	0	0	1	0	3	0	1	0
pineland	8	1	3	0	11	5	17	5	9.8	3.6
hammock	3	1	7	2	2	1	5	4	4.2	2

TABLE 5. ANT SPECIES VISITING HONEY BAITS AND NECTARIES IN EVERGLADES NATIONAL PARK. NECTAR SOURCES ARE B = BAITS OR N = NECTARIES. HABITAT TYPES ARE H = HAMMOCKS OR P = PINELANDS.

Species (all native)	nectar	habitat
<i>Aphaenogaster texana</i> var. <i>caroliniensis</i> Wheeler	B	H & P
<i>Crematogaster ashmeadi</i> Mayr	B	P
<i>Crematogaster</i> sp. nr. <i>ashmeadi</i> (undescribed)	B	P
<i>Cyphomyrmex rimosus</i> (Spinola)	B	P
<i>Pheidole dentata</i> (Mayr)	B & N	H & P
<i>Pseudomyrmex elongatus</i> (Mayr)	B & N	H
<i>Pseudomyrmex simplex</i> (F. Smith)	B & N	H & P
<i>Solenopsis geminata</i> (Forel)	B & N	H & P

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