Extrafloral nectary-mediated ant-plant interactions in the coastal vegetation of Veracruz, Mexico: Richness, occurrence, seasonality, and ant foraging patterns[1]

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Abstract: We studied the extrafloral nectary-mediated ant-plant interactions in the coastal vegetation of Veracruz, Mexico. We surveyed the richness and abundance of interactions, their correlations in both groups, the proportion of associated species and groups, and their temporal and spatial variation. Forty-three plant species (25 families) had extrafloral nectaries, which were more abundant during the wet season. Thirty-one ant species in 18 genera were found in 208 associations with extrafloral nectaries. Sixty-six percent of the nectary-bearing plant species were visited by ants. Eighty-four of the recorded ant species visited nectaries. The proportion of associated species was always higher than that of non-associated species. Ants forage on nectaries day and night, with sympatric species having contrasting foraging schedules. Abundance of nectary-bearing plants differed among seasons, while ant density and richness differed seasonally in specific vegetation types. Abundance of extrafloral nectaries was positively correlated with ant species richness during the rainy season. Seasonal patterns suggest higher nectar availability on vegetative structures during the rainy season and on reproductive structures during the dry season. The high proportion of extrafloral nectary-bearing plants found (14.82%) compared to other surveyed habitats (5-15%) suggests that extrafloral nectary-mediated plant protection by ants is a common feature in coastal communities of Veracruz.

Keywords: ant foraging patterns, ant-plant associations, coastal dune vegetation, dry tropical forest, extrafloral nectaries, seasonality.

Résumé : Nous avons étudié les interactions qui existent entre les fourmis et les plantes de la végétation côtière de Veracruz, au Mexique, interactions influencées par la présence de nectaires extrafloraux. Nous avons observé la richesse et le nombre des interactions, leurs corrélations dans les deux groupes, ainsi que la proportion et la variation temporelle et spatiale des espèces et des groupes associés. Quarante-trois espèces de plantes, appartenant à 25 familles, ont des nectaires extrafloraux. Elles sont plus abondantes durant la saison humide. Trente-et-une espèces de fourmis provenant de 18 genres forment 208 associations avec des nectaires. Les fourmis visitent 66 % des plantes porteuses de nectaires extrafloraux. Au total, 84 % des espèces de fourmis recensées visitent les nectaires. Il y a toujours une plus grande proportion d'espèces associées que d'espèces non associées. Les fourmis se nourrissent sur les nectaires de jour comme de nuit, les espèces sympatriques ayant des patrons d'activité différents. L'abondance des plantes possédant des nectaires qui attirent les fourmis change avec les saisons. Il en va de même pour la densité et la richesse des fourmis dans certains types de végétation. L'abondance des nectaires extrafloraux est corrélée de façon positive avec la richesse en espèces de fourmis pendant la saison des pluies. La disponibilité du nectar serait supérieure sur les structures végétatives pendant la saison des pluies alors qu'elle serait plus grande sur les structures reproductrices pendant la saison sèche. La grande proportion (14,82 %) de plantes avec nectaires extrafloraux qui a été trouvée, comparée à celle qui est observée dans d'autres habitats (5 à 15 %), laisse croire que la protection par les fourmis des plantes qui les portent serait une caractéristique des communautés côtières de Veracruz.

Mots-clés : associations fourmis-plantes, forêt tropicale sèche, nectaires extrafloraux, patrons d'alimentation des fourmis, saisonnier, végétation côtière de dunes.

Introduction

Many field experiments have demonstrated that ants visiting extrafloral nectaries (EFNs) and foraging from their sugary secretions promote plant defence against herbivores, increasing reproductive success of the plants (Koptur, 1984; 1985; Barton, 1986; Rico-Gray & Thien, 1989; Oliveira, 1997; Koptur, Rico-Gray & Palacios-Rios, 1998; Oliveira *et al.*, 1999), although benefit to the plant from ant visitation is not universal (O'Dowd & Catchpole, 1983; Whalen & MacKay, 1988). Despite the importance of these associations for the interacting species, ant-plant associations are usually opportunistic and rarely species-specific (Rico-Gray, 1993), are spatially and temporally variable (Bentley, 1976; Davidson, 1977b; Levings, 1983; Schupp & Feener, 1991; Koptur,

1992b; Rico-Gray, 1993; Cros, Cerdá & Retana, 1997; Díaz-Castelazo & Rico-Gray, 1998), and are highly dependent on resource attributes (Apple & Feener, 2001; Blüthgen & Fiedler, 2004; Rudgers & Gardener, 2004).

Thus, to understand the role and adaptive significance of EFN-mediated ant-plant associations in a community it is necessary to study their richness and spatial and temporal variation (including ant foraging patterns) along with the distribution of EFNs and ants in a given habitat. To our knowledge, however, seasonality and ant foraging patterns have never been studied in conjunction with the distribution of EFNs and ants in a given habitat.

Given the importance of EFNs to ants, we should expect a positive, significant correlation between the distribution of EFN-bearing plants and ants. However, few studies have addressed this in temperate or tropical environments (Bentley, 1976; Keeler, 1979; 1980; Koptur, 1992b).

Studies in Mexican coastal vegetation have shown that ants use a variety of plant-derived food resources, including EF-nectar (Rico-Gray, 1993; Rico-Gray *et al.*, 2004), and that ant visitation to EFNs can reduce herbivore damage and increase the plant's reproductive output (Rico-Gray & Thien, 1989; Oliveira *et al.*, 1999). However, quantitative, qualitative, and correlational analysis of the EFN-mediated ant-plant associations with emphasis on spatial and temporal variation could elucidate the importance of EFNs in tropical coastal communities. Community-level attributes pertaining to such systems were addressed through the following questions: How abundant are extrafloral nectaries in different vegetation types, and what proportion of extrafloral nectary-bearing plants is associated with ants? What are the composition and abundance of nectarivorous ants in different plant communities and what proportion is associated with EFNs? Are EFN-bearing plants and ant densities/richness correlated? How do associations vary across seasons and according to ant foraging patterns? The study was carried out in a series of tropical plant communities distributed on the central coast of Veracruz, Mexico.

Methods

STUDY SITE

The study was carried out at Centro de Investigaciones Costeras La Mancha (CICOLMA), along the coast of the state of Veracruz, Mexico (19° 36' N, 96° 22' W; elevation < 100 m; *ca* 70 protected ha). The climate is warm subhumid; a rainy season occurs between June and September, a dry season with cold fronts occurs from October to January (winter), and plain dry conditions occur the rest of the year. Total annual precipitation is 1,500 mm, mean annual temperature is 24-26 °C, and minimum annual temperature is 15 °C (Moreno-Casasola *et al.*, 1982; Rico-Gray, 1993). The major vegetation types are tropical dry forest, tropical deciduous forest (two subtypes), dune scrub, grassland, mangrove forest and fresh water marsh (Rico-Gray, 1993; Castillo-Campos & Medina, 2000). Approximately 290 species of flowering plants are known to occur in the reserve area (Rico-Gray, 1993), although more recent censuses estimate 139 species of trees and bushes alone (Castillo-Campos & Medina, 2000).

ABUNDANCE OF PLANTS WITH EXTRAFLORAL NECTARIES

To determine the abundance and richness of EFN-bearing plants we estimated their linear cover (portion of the transect length occupied by EFN-bearing plants) through the line-intercept technique (Pemberton, 1990) along six transects (135-375 m), each covering a vegetation type dominant in the study site (dune pioneers, dune scrub, two types of tropical deciduous forest [young soil, old soil], mangrove forest, and the fresh water marsh–deciduous forest–dune scrub ecotone), during the three seasons at the site (dry season, rainy season, and dry-cold front season). Since no vegetation replicates were available, each transect was subdivided into three discrete sections where data were collected to allow comparisons among vegetation types. An angular transformation (arc-sin) was applied to the percent cover of plants with EFNs in each transect (an estimate of the abundance of plants with EFNs).

Repeated-measures ANOVA (Statistica v.6.0; StatSoft, 1998) was used to analyze changes in the cover and richness of EFN-bearing plants for the three seasons and for the six vegetation types. Using Sorensen's similarity index (Brower & Zar, 1977) we estimated the similarity of EFN-bearing plant species among plant communities.

ABUNDANCE (DENSITY) OF ANTS AND ITS CORRELATION WITH EFNS

To determine the abundance of ants that forage on plants in the different vegetation types, we placed 45 adherent 1.5-cm diameter plastic discs (15 per transect interval) on plants at equal distances along each transect. A honey solution (50% bee honey, 50% water) was used as bait on the discs to attract potential nectar-foraging ants (since discs were placed on plants, ants that rarely forage on plants may be underrepresented in the baits), and at 30 min and 60 min after baiting we recorded the ant species present and the number of individuals per species on each disc (Bentley, 1976; Keeler, 1979; 1980; 1981). Censuses were repeated for each of the three seasons. After testing for normality and homogeneity of variances (Shapiro-Wilk's, Levene's) square-root transformations were performed on ant species richness (Fowler & Cohen, 1992).

An ant-density index based on sampling intensity was calculated for each vegetation transect since the spacing between baits among vegetation types was different (due to differences in length among vegetation transects). Thus, ant abundance at each transect interval was divided by sampling intensity (number of baits per interval/interval length). Since this index does not meet the normality assumptions, a Box-Cox transformation (JMP v.3.1.6.2.; SAS Institute, 1997) was performed prior to statistical analysis. Throughout the text the ant-density index refers to a corrected estimate of ant abundance. A repeated-measures ANOVA (Statistica v.6.0; StatSoft, 1998) was used to analyze changes in ant richness and the ant-density index for the three seasons and for the six vegetation transects. Whenever an interaction between season (repeated-measures) and vegetation was found, Tukey HSD tests were performed to explore in which season and in which transect the differences were found.

To dismiss the possibility of spatial autocorrelation among ant sampling points on each transect, a local spatial autocorrelation analysis based on Gi(d) and Gi×(d) statistics (ROOKCASE v.0.9.5.a; Sawada, 1999) was performed on the original ant abundance data. To explore the association between the cover of EFN-bearing plants and the density and richness of nectar foraging ants, the product-moment correlation coefficient of Pearson (Fowler & Cohen, 1992) was estimated using Statistica v. 6.0 (StatSoft, 1998).

EFN-MEDIATED ANT-PLANT ASSOCIATIONS AND ANT FORAGING PATTERNS

To detect all EFN-bearing plants visited by ants (EFN-mediated ant-plant associations), the six vegetation transects were surveyed every 4 months (seasonally), day and night, for 2 y. To locate EFN-bearing plants, we used available taxonomic lists (Elias, 1983; Oliveira & Leitão-Filho, 1987; Oliveira & Oliveira-Filho, 1991; Koptur, 1992b) and previous reports for the area (Rico-Gray, 1993). We also inspected plants more carefully where we observed stereotypical nectar-feeding behaviour of ants (Keeler, 1979; Rico-Gray, 1993) or the presence of sooty molds on or around the glands, which indicates secretion of sugar solutions (Pemberton, 1990). Simultaneously, we detected and observed nectar-foraging ants, recording the species, the number of individuals per species, and the location of the nectaries. A small number of ants and plants were collected for further identification (Departamento de Entomología and XAL Herbarium, Instituto de Ecología, A.C.).

PROPORTION OF ASSOCIATED SPECIES

Censuses of ants feeding on EFNs (EFN-mediated ant-plant associations) were performed simultaneously with the baiting experiments (estimating density and richness of potential nectarivorous ants) and the estimates of EFN abundance (% cover of plants with EFNs). These censuses were repeated in each season to estimate the proportion of ants and EFN-bearing plants associated to each other.

A *t*-test was used to compare the frequencies of day and night visits by ants (Sokal & Rohlf, 1995). We performed a 6×2 contingency table to test (χ^2) the independence between ant activity patterns and vegetation types (Statistica software v. 6.0; StatSoft, 1998). We used Mann-Whitney *U*-tests to determine the differences between the proportion of plant species visited by ants and the proportion of ants associated to EFN-bearing plants. Kruskall-Wallis tests allowed us to detect seasonal and vegetational differences in the proportions of associated ant and plant species (Fowler & Cohen, 1992).

Results

ABUNDANCE OF PLANTS WITH EFNS

We recorded 43 EFN-bearing plant species in the different plant communities surveyed (Appendix I). Plant cover of EFN-bearing plants was greater in the rainy season relative to the dry and dry-cold front seasons ($F_{2, 24} = 4.214$, $P < 0.05$), but did not differ among vegetation

types. Richness of species with EFNs was also greater in the rainy season ($F_{2, 24} = 4.249$, $P < 0.05$) and differed among vegetation types ($F_{5, 12} = 5.029$, $P = 0.01$), being greater in the deciduous forest growing on old soil.

The similarities between plant communities of EFN-bearing plant species are shown in Table I. The dune scrub and the tropical deciduous forest (young soil) were the most similar vegetation types, sharing 50% of their species, whereas the dune pioneers and the fresh water marsh–deciduous forest (old soil) ecotone shared no species of plants with EFNs.

ABUNDANCE (DENSITY) OF ANTS AND CORRELATION WITH EFNs

Thirty-one ant species (5 subfamilies, 18 genera) were found on the baits on plants and thus were considered potential nectar foragers (Table II). Mean values of ant density in each vegetation-season combination (factors) and their significant differences (Tukey HSD test) are shown in Figure 1a. The interaction between season and vegetation was significant for ant density ($F_{10, 24} = 3.593$, $P < 0.005$), which was consistently low in mangrove forest relative to other vegetation types during the three seasons. Similarly, deciduous forest on young soil had low ant densities relative to other vegetation types for the rainy and the dry seasons. In contrast, dune pioneer vegetation had high ant densities relative to other vegetations types during the dry-cold front and dry seasons. Deciduous forest growing on old soil had similar ant densities relative to other types during the rainy and the dry seasons. If we focus on seasonal differences in ant densities, the dry-cold front season had the lowest values relative to the dry season in all vegetation types except those of dune scrub and deciduous forest on young soil. Ant densities for the dry-cold front season are also different from those found in the rainy season in the old soil-deciduous forest.

Richness of ant species showed a less strong, but still significant ($F_{10, 24} = 2.42$, $P < 0.05$) season-vegetation interaction. One evident pattern (Figure 1b) is the lower ant richness found in the mangrove forest (relative to dune pioneer vegetation and both deciduous forests) for the dry-cold front season. Notice also the low ant richness found during the dry-cold front season relative to the other seasons, particularly in the mangrove forest. In contrast, ant species richness is the same for the rainy and dry seasons in all the vegetation types.

TABLE I. Floristic similarity of EFN-bearing species among vegetation types.

Vegetation types	DP[a]	DS	DFO	DFY	MFS	MG
DP	—					
DS	40	—				
DFO	8	7.41	—			
DFY	18.18	50	25.81	—		
MFS	0	16.67	41.38	23.08	—	
MG	7.41	34.48	43.75	19.35	38.71	—

[a] DP = dune pioneers, DS = dune scrub, DFO = tropical deciduous forest on old soil, DFY = tropical deciduous forest on young soil, MFS = ecotone among fresh water marsh–deciduous forest–dune scrub, MG = mangrove forest.

TABLE II. Ant species and number of plant species visited with extrafloral nectaries[a].

Ant species	Number of plant species visited	
MYRMICINAE		
Cephalotes minutus		7
Crematogaster brevispinosa		8
Forelius pruinosus		4
Leptothorax echinatinodis		3
Monomorium cyaneum		4
Monomorium pharaonis		2
Pheidole sp.		5
Solenopsis geminata		4
Tetramorium spinosum		6
Wasmannia auropunctata		4
FORMICINAE		
Brachymyrmex sp.	2	
Camponotus atriceps		28
Camponotus hirsutinasus		4
Camponotus mucronatus		15
Camponotus planatus		23
Camponotus sp.	3	
Paratrechina longicornis		13
Paratrechina sp.		5
DOLICHODERINAE		
Azteca sp.	8	
Dolichoderus diversus		2
Dolichoderus lutosus		26
Dorymyrmex bicolor		5
PSEUDOMYRMYCINAE		
Pseudomyrmex elongatus		1
Pseudomyrmex ferrugineus		1
Pseudomyrmex gracilis		8
Pseudomyrmex pallidus		2
Pseudomyrmex sp. 1		4
Pseudomyrmex sp. 2		1
Pseudomyrmex brunneus		4
PONERINAE		
Pachycondyla unidentata		3
Pachycondyla villosa		7

[a] One ant species (*Cyphomyrmex* sp., Myrmicinae) was observed on honey baits but not associated with EFN-bearing plants.
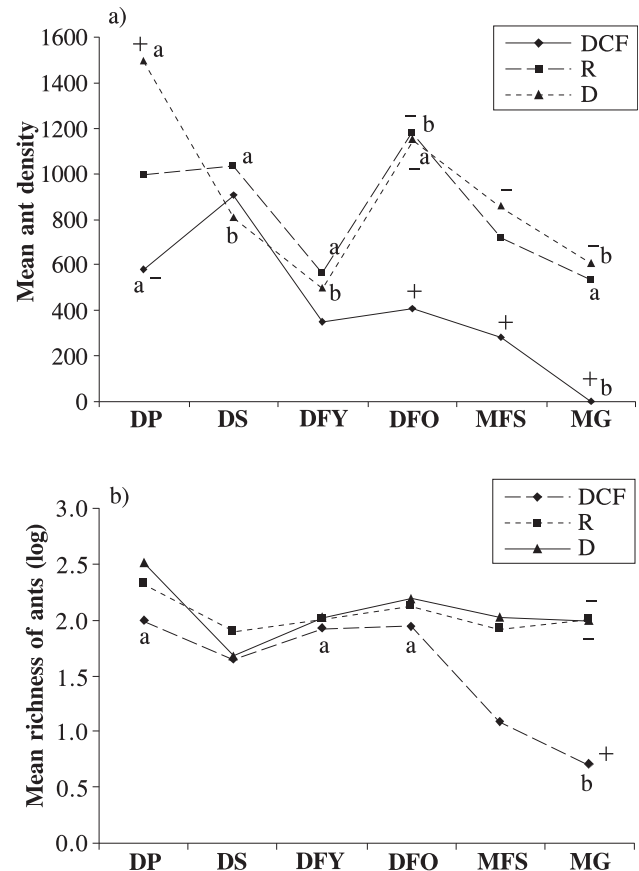

FIGURE 1. Mean values of ant density index (a) and ant species richness (b) for vegetation types and seasons. Significant differences at $P < 0.05$ (Tukey HSD test) for factor interactions are shown among vegetation types within a season as a) and b) and among seasons within vegetation types as (+) and (-). Seasons: DCF = Dry with cold fronts, R = Rainy, D = Dry. Vegetation types: DP = Dune pioneers, DS = Dune scrub, DFY = Tropical deciduous forest on young soil, DFO = Tropical deciduous forest on old soil, MFS = Ecotone among fresh water marsh-deciduous forest-dune scrub, MG = Mangrove forest.

There was no local spatial autocorrelation between contiguous ant sampling points (baits) in any of the vegetation transects. When percent cover of EFN-bearing plant species in each vegetation type was considered for each season separately, the abundance of EFN-bearing plant species was significantly and positively correlated with ant species richness during the rainy season ($r = 0.83$, $P < 0.05$). No correlation was found when percent cover of plants with EFNs was considered for all the seasons together.

EFN-MEDIATED ANT-PLANT ASSOCIATIONS AND ANT FORAGING PATTERNS

We recorded 43 EFN-bearing plant species and 31 ant species in 208 associations (Table II, Appendix I). While ants visited EFN-bearing plants day and night, species composition varied between periods (Figure 2). The frequency of ant species (*i.e.*, the number of times an ant species is associated with or visiting EFN-bearing plants) was higher during the day than at night ($t = 5.58$, $P < 0.01$, $n = 6$); however, ant density did not differ between sampling periods.

The ant genus *Camponotus* was the best represented, both in terms of species and individuals. *Camponotus atriceps* was the ant species that visited the most EFN-bearing plant species (28). The most frequent and abundant ant species differed in their activity patterns (Figure 2). These patterns did not depend on vegetation type, remaining as described for the different plant communities ($\chi^2 = 4.1450$, df = 5, $P = 0.5$). Three ant species in the genus *Pseudomyrmex* appeared to specialize, foraging on the EFNs of only one plant species.

The frequency of ant visits and ant species richness on the most frequently visited EFN-bearing plant species are shown in Figure 3. Twenty-five plant families exhibited EFNs, of which 23 exhibited one to three EFN-bearing species visited by ants; Leguminosae was the plant family with the most species (7) involved in EFN-mediated associations with ants (Appendix I).

PROPORTION OF ASSOCIATED SPECIES

We recorded EFNs in 14.82% of the angiosperm species reported (43 of 290) for the different vegetation types studied. Sixty-six percent of the EFN-bearing plant
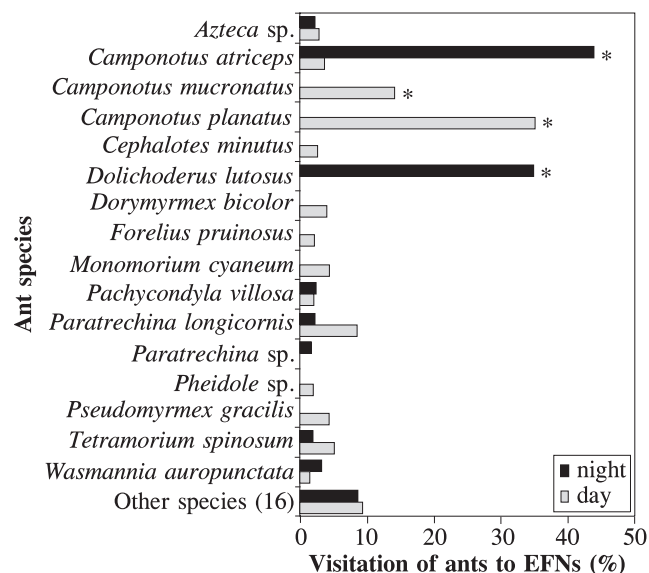
FIGURE 2. Ant visitation to EFN-bearing plants (% of visit frequencies of ants to plants with EFNs) for day and night periods. Asterisks (*) indicate the ant species that are more frequently associated to EFNs; note contrasting activity patterns.

species (46% of individuals) were visited by ants, and in every census the proportion of plant species visited by ants was higher than that of non-visited species ($U = 298$, $P < 0.001$, $n = 18$). However, no differences were found when comparing proportions of visited plants rather than species. The proportion of plant species visited by ants was higher during the rainy season ($K = 6.37$, df = 2, $P < 0.05$); this tendency was maintained across vegetation types.

Eighty-four percent of the ant species were observed visiting EFNs. In every census, the proportion of ant species associated with plants was higher than that not associated with plants ($U = 324$, $P < 0.001$, $n = 18$). The proportion of ant species associated with plants was higher during the rainy season, relative to the dry and dry-cold front seasons ($K = 7.88$, df = 2, $P = 0.05$); this tendency was maintained across vegetation types. The higher proportion of associated ant species relative to that of not associated species was maintained both among vegetation types and seasons ($^2 = 27.29$, df = 17, $P = 0.5$).

Discussion

ABUNDANCE OF ANTS AND EFN-BEARING PLANTS AND CORRELATIONS

The differences found for all bait-obtained ant variables (richness, density) among seasons were the result of their small values during the dry-cold front season, particularly in the mangrove forest. The dry-cold front season marks the beginning of the dry period (October) in the study sites with an abrupt decrease in precipitation, a decrease in temperature (see Figure 1a of Rico-Gray *et al.*, 1998), and an increasing intensity of northern cold winds from November to February (Blain, 1988). In such conditions, it is reasonable to expect a decrease in ant activity and forager density (or ant species richness) on plants. Although reduced precipitation also occurs during the dry season, a higher temperature relative to the dry-

cold front season (see Figure 1a of Rico-Gray *et al.*, 1998), the absence of cold winds, and a general flowering peak (Bullock & Solís-Magallanes, 1990) that offers new resources to ants such as flower nectar, nectar from reproductive structures, and arthropod prey could explain the increased ant activity on plants (density, richness). In fact, the number of ant associations with reproductive structures and flowers found at the study site by Rico-Gray (1993) peaks during the dry season.

In this study, ant species richness was the only ant variable positively correlated with the abundance of EFN-bearing plants, specifically in the rainy season. Ant richness, in particular, has been correlated with the primary productivity of a habitat, commonly increased by precipitation (Davidson, 1977a). Keeler (1980) found that ant species richness was the ant variable most highly correlated with the abundance of EFNs in temperate plant communities. The same is true for our study during the increased primary productivity of the rainy season: when EFNs are more abundant and/or active, more ant species exploit them.

EFN-MEDIATED ANT-PLANT ASSOCIATIONS AND ANT FORAGING PATTERNS

EFN-mediated ant-plant associations were also higher during the rainy season. In tropical seasonal environments most plant species simultaneously produce new leaves at the onset of the rainy season (Levings, 1983; Bullock & Solís-Magallanes, 1990), and EFNs increase their secretory activity during this period of fast leaf growth and high risk of herbivore attack (Bentley, 1976; 1977; Elias, 1983; Koptur, 1992a; Rico-Gray, 1993; Rico-Gray *et al.*, 2004). Furthermore, EF nectar (coupled with homopteran honeydew) has been regarded as the main liquid-energy food source for ants during the rainy season in the study site (Rico-Gray, 1993).

The richness of associations between ants and EFN-bearing plants was particularly high (208 associations), especially in view of the 312 ant-plant associations (considering a wider array of liquid-energy food sources) previously recorded for the same area (Rico-Gray, 1993). Moreover, if we focus only on EFN-mediated ant-plant interactions, the richness of associations found by Rico-Gray (1993) could be an underestimate, since no nocturnal observations were performed. Our night censuses revealed a segregation of activity schedules by different ant species: some ant species were strictly nocturnal, and some EFN-bearing plants were visited by ants only at night.

Individuals in the ant genus *Camponotus* (Hölldobler & Wilson, 1990), the predominant ant genus worldwide, were the most numerous visitors of EFNs, a common observation for tropical, subtropical, and temperate habitats (Rico-Gray, 1989; Oliveira & Brandão, 1991; Rico-Gray, 1993; Rico-Gray *et al.*, 1998). Our results showed that *C. planatus* and *C. atriceps*, the most frequent ant species on EFN-bearing plants, exhibit contrasting (diurnal/nocturnal) activity patterns in all the vegetation types, suggesting a temporal partitioning in the use of EF nectar (Oliveira *et al.*, 1999; Brown, 2000). The possible interference in resource use between these two sympatric species may be diminished by their differences in physio-
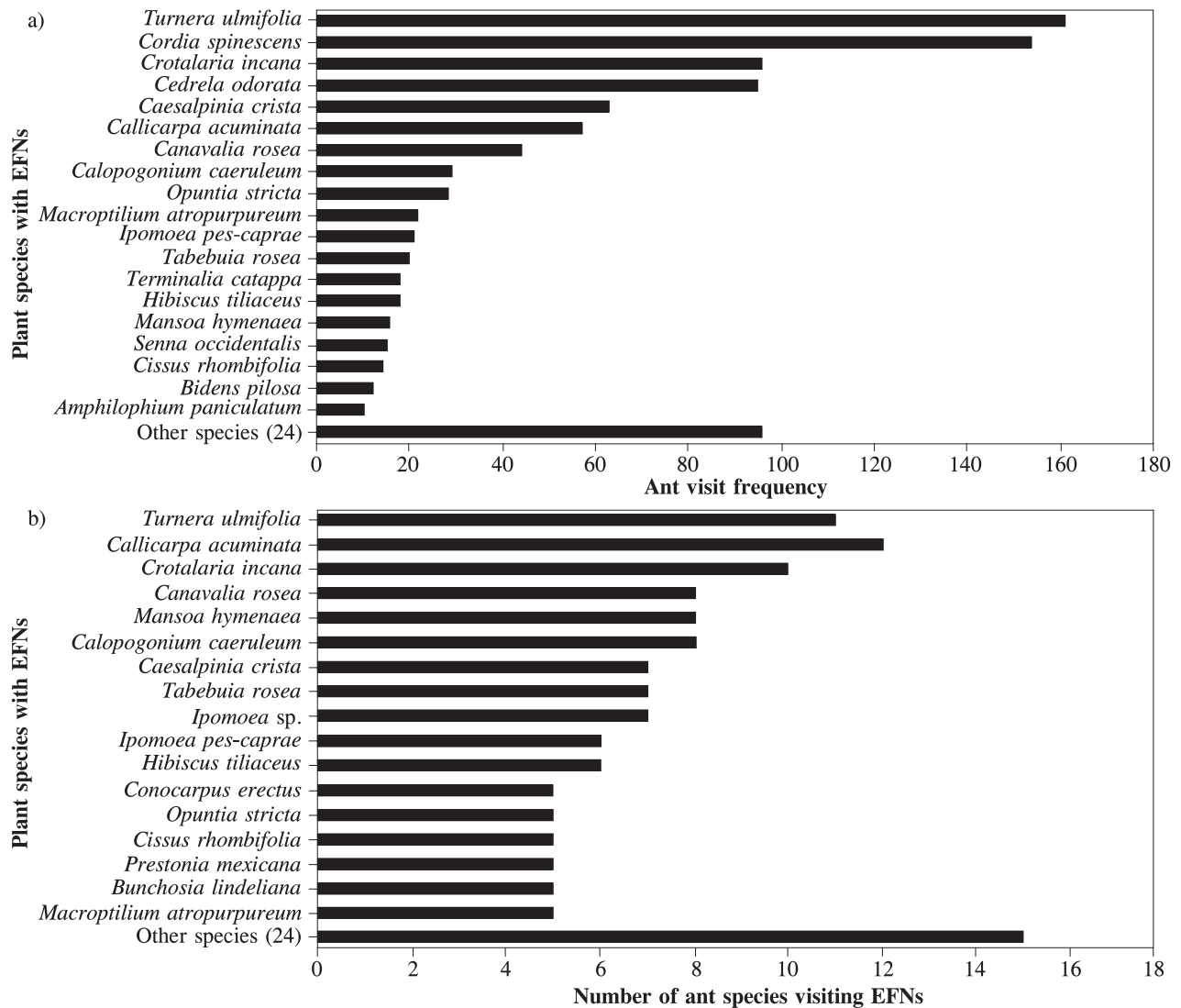
FIGURE 3. a) Number of ant visits to the most frequently visited plants with EFNs (regardless of number of ant foragers/species per visit), b) Richness of ant visitors to EFN-bearing plant species (only plant species with the highest richness of ant visitors are shown).

logical tolerances to temperature and humidity (Levings, 1983; Torres, 1984; Cros, Cerdá & Retana, 1997; Cerdá, Retana & Cros, 1998; Oliveira *et al.*, 1999).

Species-specific associations between ants and EFN-bearing plants were only detected for *Pseudomyrmex* ant species (*P. ferrugineus*, *P. elongatus*, and *P.* sp.2); this ant genus is the most primitive and the most commonly (20% of extant species; Ward, 1990) associated with myrmecophytic plants.

PROPORTION OF ASSOCIATED SPECIES

The proportion of EFN-bearing plant species at the coastal plant communities we studied lay in the upper limit (14.82%) of those reported previously for both tropical and temperate habitats (5-15%; Koptur, 1992b). The importance of extrafloral nectar as a food resource for ants is clear, since 66% of the species and 46% of the individuals of EFN-bearing plants were visited by ants, and 84% of the local ant species were registered as nectar foragers. When we estimated the proportion of ant species

not associated with EFNs, those ants that rarely forage on plants were excluded since baits were placed on plants (with or without EFNs). However, the proportion of associated ant and plant species was evidently higher in the rainy season, and it was constantly (throughout seasons and vegetation types) higher than the proportion of non-associated ant and plant species. This indicates that EFN-mediated ant-plant associations are not simply the effect of an elevated abundance or richness of plants with EFNs and nectarivorous ants.

CONCLUDING REMARKS

The spatial and temporal variation in EFN-mediated ant-plant associations found suggests that the potential for ant-derived benefits for EFN-bearing plants may vary as well. Since ant (and herbivore) densities could determine the outcomes of the association (Beattie, 1985; Barton, 1986), we suggest that in plant communities where "nectarivorous" ant densities are high (*i.e.*, dune pioneer vegetation, dune scrub, deciduous forest on old soil) increased

reproduction of certain plant species derived from their association with ants may take place mediated mainly by EF nectar of vegetative structures during the rainy season and by EF nectar of reproductive structures during the dry season. There is evidence of mutualistic interactions of two plant species with ants (and other EFN visitors) in one of these "high-association" communities, dune scrub (Oliveira *et al.*, 1999; Torres-Hernández *et al.*, 2000; Cuautle & Rico-Gray, 2003). Apart from these examples, the densities of herbivores, their impacts on plants, and the deterrent effectiveness of different ant species in these communities are not known. Data of this type must also combine data on EF nectar investment by plants through nectary traits (Blüthgen & Fiedler, 2004; Rudgers & Gardener, 2004) - an aspect we are currently working on - in order to complete the guideline map of opportunities for mutualism in the plant communities of coastal Veracruz.

Acknowledgements

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APPENDIX I. EFN-bearing plant species and associated ant species (see Table I) for the different coastal vegetation types studied in Veracruz, Mexico.

Family/ Species	Ant species	Season	Vegetation type	Site of EFN
AMARANTHACEAE				
Iresine celosia [3]	12	DCF	DP, DFO	5a
APOCYNACEAE				
Prestonia mexicana [4]	7, 12, 15, 21, 31	D, R	DFY, DFO	1a, 4c
ASCLEPIADACEAE				
Gonolobus barbatus [4] *	21	D	MFS, MG	1a
BIGNONIACEAE				
Amphilophium paniculatum [4]	1, 12 19, 21	D, R, DCF	DS, DFY	1a, 6, 6a, 8
Mansoa hymenaea [4]	7, 8, 10, 12, 21, 25, 27, 31	D, R, DCF	DFO	4b
Tabebuia rosea [1]	2, 10, 12, 13, 15, 14, 21	D, R, DCF	MFS, DFO	1a, 1c
BORAGINACEAE				
Cordia spinescens [2]	1, 2, 5, 12, 13, 15, 14, 16, 17, 18, 20, 21, 30, 31	D, R, DCF	MFS, DS	1a, 1c
Cordia dentata [1]	9, 18	R	MG	1a, 1c
CACTACEAE				
Opuntia stricta var. *dillenii* [5]	2, 12, 15, 17, 21	D, R, DCF	DS	9
CAPPARIDACEAE				
Capparis baducca [2]	15	DCF	DFO	1, 4a, 8
Crataeva tapia [1] *	15	R	DFO, MFS	1a, 4a
COMBRETACEAE				
Conocarpus erectus [1]	2, 12, 14, 21, 31		MG	2
Terminalia catappa [1]	9, 12, 14		MG	2
COMPOSITAE				
Bidens pilosa [3]	9, 14, 18	R	MG, DP	4a, 4b, 7
CONVOLVULACEAE				
Ipomoea pes-caprae [4]	4, 12, 15, 11, 17, 22,	D, R	DP	2
Ipomoea sp. [4]	1, 12, 13, 14, 17, 21, 29	R, DCF	MG	2
CUCURBITACEAE				
Sicydium tamnifolium [4]	15, 14, 21	D, DCF	MFS	2
GRAMINEAE				
Arundo donax [3]	12, 15, 17	D	DP	4b
LEGUMINOSEAE				
Acacia cornigera [2]	21, 24	D, R, DCF	MFS, DFO	1c
Caesalpinia crista [2]	4, 12, 15, 16, 22, 25, 29	R, DCF	DP, DS	3, 5a, 7
Calopogonium caeruleum [3]	9, 12, 15, 14, 21, 25, 27, 29	D, R, DCF	MFS, MG, DS	3, 4c
Canavalia rosea [4]	4, 8, 12, 15, 17, 18, 22, 29	D, R, DCF	DP	4a, 5, 5a, 10
Chamaecrista chamaecristoides [2]	3, 12	R	DS, DFY	1c
Crotalaria incana [3]	1, 3, 12, 15, 14, 17, 19, 21, 22, 25	D, R, DCF	DS	3, 6a, 10
Macroptilium atropurpureum [4]	15, 14, 17, 19, 21	DCF	DS, DP, MG	3, 4c, 5, 6, 8
Senna occidentalis [2]	9, 12	R	MG	1c, 4a
MALPIGHIACEAE				
Bunchosia lindeniana [1]	2, 7, 12, 15, 21	DCF	DFO	1c, 4b
Bunchosia biocellata [1] *	21	D	MFS	1c, 4b
MALVACEAE				
Hibiscus pernambucensis [1]	3, 8, 12, 15, 17, 22	D, R, DCF	DP	1c, 6
MELASTOMATACEAE				
Heterocentron subtriplinervium [2]	31	R	MG	1, 2
MELIACEAE				
Cederlla odorata [1]	2, 5, 6, 7, 9, 10, 12, 13, 15,14, 16, 18, 19, 21, 25, 26, 28, 30, 31	D, R, DCF	MFS, MG	1c, 4
Trichilia havanensis [2]	14, 21	D, R, DCF	MFS	6a, 8
MORACEAE				
Ficus obtusifolia [1]	14, 19	DCF	MFS	1a, 4c
PASSIFLORACEAE				
Passiflora holosericea [4]	2, 12, 17	D, DCF	DS	2
PHYTOLACCACEAE				
Petiveria alliaceae [3]	8, 15, 21	D, R	DFO	4a, 4c, 5a

APPENDIX I. Continued.

Family/ Species	Ant species	Season	Vegetation type	Site of EFN
POLYGONACEAE				
Coccoloba barbadensis [1] *	21	D	DFO	1a, 4c
SOLANACEAE				
Solanum rudepanum [2]	12	D	MFS	1a
Solanum sp. [2] *	21	D	MFS	1a
TURNERACEAE				
Turnera ulmifolia [2]	1, 3, 5, 12, 15, 11, 17, 19, 20, 21, 25	D, R, DCF	DS	2
VERBENACEAE				
Callicarpa acuminata [2]	1, 2, 5, 7, 12, 15, 14, 17, 19, 21, 27, 30	D, R, DCF	MFS, DFO, DFY	1a
Cornutia grandiflora [2]	12, 14	D	DFY	1a
Petrea volubilis [4]	1, 15, 26	R	DFO	1a
VITACEAE				
Cissus rhombifolia [4]	12, 15, 17, 21, 25	R, DCF	DFY	3

Plant life-form: [1]tree, [2]shrub, [3]herb, [4]vine, [5]cacti. Plants visited only at night = *. Season: D = dry (February-May), R = rain (June-September), DCF = dry-cold fronts (October-January). Vegetation types as in Table I. Site of EFN (as in Koptur, 1992a, with some modifications when required): 1 = leaf, 1a = leaf blade, 1b = blade base, 1c = raquis or midvein, 2 = petiole, 3 = stipules and/or stipels, 4 = stems, 4a = leaf axils, 4b = nodes, 4c = shoots, 5 = pedicels, peduncles, or stems of inflorescence, 5a = spike, 6 = petals or sepals, 6a = flower buds, 7 = bracts, 8 = on fruit, capsule, or pod, 9 = areoles, 10 = aborted flowers or bud scars.