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Interaction between ants and orchids in the Soconusco region, Chiapas, Mexico.

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Abstract

Damon A, Pérez-Soriano MA. 2005. Intereaction between ants and orchids in the Sonocusco region, Chiapas, Mexico. Entomotropica 20(1): 59-65.

Ants were seen to visit extrafloral nectar sources mostly on the flower bases and petiole junctions of *Encyclia cordigera*, *E. chacaoensis* and *E. belizensis* var. *parviflora* and the production of extrafloral nectar in relation to the presence of ants was observed during the flowering periods of these orchids in the Regional Botanical Garden "El Soconusco" and the orchidarium Santo Domingo, in Chiapas, Mexico. Ants were also seen to feed on secretions produced at flower bases and on the surface tissue and tips of buds of *Catasetum integerrimum* and *Cycnoches ventricosum*. Mention is included of ants associated with other species of orchids collected in the field. Eleven species of ants were fully identified out of a total of 19 species collected. Most species were common inhabitants of secondary vegetation, with some species registered as pests in agroecosystems and human dwellings. It was not clear how the plants benefited by investing scarce resources in the provision of food to attract ants, but a defense role is possible for one species, *Camponotus novogranadensis*, which was observed to be aggressive when the plant was disturbed by touching during visits to the extrafloral nectaries of *E. chacaoensis*. It is suggested that *E. belizensis* var. *parviflora* benefits from the presence of *Crematogaster* aff. *torosa* resident in old pseudobulbs, which effectively act as domatias, by absorbing nutrients from organic wastes produced by those ants.

Additional key words: Ants, mutualism, orchids, extrafloral nectar, reproductive structures.

Resumen

Damon A, Pérez-Soriano MA. 2005. Interacciones entre hormigas y orquídeas en la region de Sonocusco, Chiapas, México. Entomotropica 20(1): 59-65.

Observamos hormigas visitando fuentes de néctar extraflorales en la base de las flores y la unión de los pecíolos de *Encyclia cordigera*, *E. chacaoensis* y *E. belizensis* var. *parviflora,* también observamos la producción de néctar extrafloral en la relación con la presencia de hormigas durante el período de floración de estas orquídeas en le Jardín Botánico Regional "El Sonocusco" y el orquidiario Santo Domingo, en Chiapas, México. También observamos hormigas alimentándose en las secreciones de la base de las flores, en el tejido superficial y en los ápices de los retoños de *Catasetum integerrimum* y *Cycnoches ventricosum*. Hacemos mención de observaciones de hormogas asociados con otras especies de orquídeas en el campo. De un total de 19 especies de hormigas colectas, 11 fueron identificadas hasta especie. La mayoria de las especies son habitantes comunes de vegetación secundaria, con algunas especies registradas como plagas en agroecosistemas ó en viviendas. No está claro cómo las plantas se benefician al invertir recursos escasos al proveer alimento para atraer hormigas, pero al menos en el caso de una especie, *Camponotus novogranadensis*, es posible que exista un rol defensivo ya que se evidenció un comportamiento agresivo cuando se tocaba la planta (*E. chacoensis*) y esta especie estaba visitando nectarios extraflorares. Se sugiere que *E. belizensis* var. *parviflora* se beneficia de la presencia de *Crematogaster* aff. *torosa* residentes en seudobulbos viejos, que fungen como domacios absorviendo nutrientes de desechos orgánicos producidfos por estas hormigas.

Palabras clave adicionales: Hormigas, mutualismo, orquídeas, nectar extrafloral, estructuras reproductivas.

Introduction

The state of Chiapas, in the southeast of Mexico is renowned for its biodiversity and also for its social, political and economic problems that have led to serious environmental deterioration in recent decades. Within this scenario, orchids are disappearing at an alarming rate and only small fragmented populations persist in the wild. The project "Ecology and rustic, sustainable production of orchids" based in "El Colegio de la Frontera Sur (ECOSUR)", in Tapachula, Chiapas is dedicated to the study of key aspects of the ecology and cultivation of native orchids, aimed at the conservation and recovery of these plants and the ecosystems that support them.

Very few studies have been carried out on the ecology of the estimated 25,000- 30,000 members of the orchid family (Pridgeon, 2000), and studies on the tropical

epiphytic species are particularly scarce, possibly due to the inaccessibility and rarity of many of these plants. In particular, little attention has been paid toward the implications of the presence of ants that are frequently seen patrolling the surface of the reproductive structures of orchids and of the nature of the secretions produced by these plants (but see Jeffrey *et al*., 1970). The characteristics of ants which have permitted the development of the varied and intricate mutualistic interactions with plants that are of vital importance to the persistence of tropical forest ecosystems are widely discussed in the literature (Wilson, 1971; Bentley, 1977: Janzen, 1977; Beattie, 1985; Holldobler and Wilson, 1990; Huxley and Cutler, 1991; Madden and Young, 1992; Blüthgen, 2003; Davidson *et al*., 2004, etc.). Dietary flexibility, based on a requirement for soft or liquid food which incurs no damage to plant tissue, has permitted ants to enter into close and often mutualistic relationships with plants, wherein ants may remain fixed on a preferred plant but forage temporarily off that "base" plant during periods of resource deficiency (Rico-Gray, 1993). The majority of studies upon ant-plant mutualism have attempted to show that ants defend their host plants against herbivores in exchange for a secure and complete food source which can be presented as extrafloral nectar (EFN) or different categories of food bodies (Janzen, 1966 and 1969); this may be particularly important for monocotyledonous plants, such as orchids, that cannot repair tissue damaged by herbivory (Almeida & Figueiredo, 2003). Such behavior has been observed in the case of species within the orchid genus *Coryanthes* (Walters & Bergold, 2001) and ants present on the surface of plants of *Encyclia cordigera* (Kunth) Dressler were found to be predators of insects with a beneficial net effect, in favor of the orchid. One of the very few detailed studies was carried out by Almeida & Figueiredo (2003) on the interaction between the epiphytic orchid *Epidendrum denticulatum* Jacq. and *Camponotus sericeiventris* (Guérin-Méneville) (Formicinae) and *Ectotomma tuberculatum* (Olivier) (Ponerinae). They concluded that ants protected reproductive structures during the relatively long flowering periods which are associated with low visitation rate by pollinators, which is characteristic of the majority of orchid species.

Extrafloral nectaries (EFNs) are found in 68 families of plants (Elias, 1983), are not directly involved in pollination strategies and offer sweet secretions which attract the attention of ants and give rise to interactions of various intensities from casual visits to obligate mutualism. The fact that ants are rarely seen in the role of pollinators is widely discussed in the literature (e.g. Janzen, 1969; Beattie, 1985; Puterbaugh, 1998), they have been reported to secrete antibiotic substances that inhibit pollen tube germination and, more recently, Ghazoul (1999) reported that ants were deterred by repellants in the floral tissue of many plants. EFN, therefore, offers plants a way of attracting and co-opting the services of ants without interfering with pollinators. The literature mentions 36 genera of orchids, the vast majority of which are epiphytic, which produce EFN usually associated with reproductive structures (Peakall 1994). *Caularthron* (*Diacrium*) *bilamellatum* (Reichb.f.) R.E. Schultes is the only orchid known to present EFNs on non reproductive structures, in this case on the leaves (Fisher *et al*. 1990); this species has been seen by the author to deteriorate in the absence of ants.

In the most developed examples of ant-plant mutualism, the plant may also offer refuges or nesting sites, termed domatia (Koptur 1984; Keeler, 1989; Rico Gray *et al*., 1989) and accumulations of organic matter derived from ant activity within these structures may serve as a nutritional source for the host plants. The literature includes mention of various species of orchids that maintain colonies of ants within old, hollow pseudobulbs or sustain ants patrolling the surface of the plant, such as species of *Cattleya*, *Coryanthes*, *Dendrobium*, *Oncidium*, *Schomburgkia*, *Vanda* and *Vanilla* (Beattie, 1985; Hölldobler & Wilson, 1990).

This study sought to observe in detail the daily and long term activity of ants in relation to the reproductive phenology and EFN production of *Encyclia cordigera* (Kunth) Dressler, *Encyclia chacaoensis* (Reichb.f.) Dressler and *Encyclia belizensis* var. *parviflora* (Regel) Dressler & Pollard. Brief observations were also carried out on *Catasetum integerrimum* Hook y *Cycnoches ventricosum* Bateman and a few species of ant were found associated with orchids collected in the field in the coastal region of Soconusco. Attempts were made to identify all of the ant species collected. These five orchid species are all found in the region of Soconusco, in the state of Chiapas, southeast Mexico. *E. chacaoensis* is now the most common, weedy and opportunistic species in the region, found from 10-1000 masl; *E. cordigera* is found on mature trees in the better conserved pastures and coffee and cocoa plantations from 10-500 masl and *E. belizensis* var. *parviflora* and the very similar *E. adenocarpa* (La Lave & Lex.) Schltr. are coastal species and are now exceedingly rare in the region due to the destruction of the narrow belts of low spiny forest that used to line the mangrove swamps where these orchids thrive. *C. integerrimum* is a weedy species found in varying habitats at lower altitudes and prefers rotting wood. *C. ventricosum* is a beautiful and now relatively rare orchid, which prefers shaded natural forest at low altitudes but can also be found in traditional coffee and cocoa plantations. *C. integerrimum* and *C. ventricosum* are both deciduous species.

Table 1. Ant species found associated with orchids in the region of Soconusco.

Species	Subfamily	Tribe
Tapinoma melanocephalum (Fabricius, 1793)	Dolichoderinae	Tapinomini
Dolichoderus debilis Emery 1890		Dolichoderini
Camponotus novogranadensis Mayr 1870	Formicinae	Camponotini
Camponotus elevatus Forel 1899		
Camponotus aff. *planatus* Roger 1863		
Camponotus aff. *guatemalensis* Forel, 1884		
Camponotus sp. 1 and 2		
Crematagaster aff. *carinata* Mayr 1862	Myrmicinae	
Crematogaster aff. *torosa* Mayr 1870		
Crematogaster sp. 1 and 2		
Cyphomyrmex rimosus (Spinola 1851)		
Monomorium floricola (Jerdon 1851)		
Pheidole gouldi Forel 1886		
Pheidole anastasii Emery 1896		
Solenopsis germinata (Fabricius, 1804)		
Wasmannia auropunctata (Roger 1863)		
Pseudomyrmex gracilis (Fabricius, 1804)	Pseudomyrmecinae	Pseudomyrmecini

Materials and Methods

Study sites: Ant activity was observed in the Regional Botanical Garden "El Soconusco" at 80m.a.s.l. in the municipality of Tuzantán (Site 1) and in the orchidarium Santo Domingo at 900m.a.s.l. in the municipality of Unión Juárez (Site 2), both in the state of Chiapas, southeast Mexico. Collecting trips were carried out in rural areas surrounding the two study sites.

Identification of ants: Ant samples collected from all five species subjected to detailed study, and those collected in the field, were sent to the Institute of Ecology A.C. in Xalapa, Veracruz, for identification.

Observations of ant behavior on the reproductive structures of *E. chacaoensis*, *E. cordigera*, *E. belizensis* var. *parviflora* were carried out during the flowering period of these three species, every fifteen days, from 11/04/03 to 28/06/03. A total of 32 plants that demonstrated ant activity were selected and marked to facilitate continued recognition during the study period (8 *E. belizensis* var. *parviflora*, 8 *E. chacaoensis* and 6 *E. cordigera* in Site 1 and 5 *E. chacaoensis* and 5 *E. cordigera* in Site 2).

Observations consisted of: 1. Structures patrolled by the ants; 2. Feeding sites of the ants, such as buds, fruits, flower bases, petiole junctions; 3. Signs of EFN production; 4. Presence of domatias; 5. Interaction of visiting ants with other insects, such as passivity, aggression or escape; 6. No. of species of ant present on the plant; 7. The no. of ants that visited the observed feeding sites during five minutes, every two hours, between 08.00 and 18.00hrs. Ants were considered to be feeding when they remained stationary for several seconds with the mouth in contact with the surface of the orchid.

Results

Identification of ants:

A total of 19 species of ants were found associated with 9 species of orchids in the region of Soconusco during the period of study (Table 1). A total of 12 species of ants were associated with the reproductive structures of *E. cordigera*, *E. chacaoensis* and *E. belizensis* var. *parviflora* and two species were associated with the reproductive structures of each of *Cycnoches ventricosum* and *Catasetum integerrimum* (Table 2a). The ant species most commonly associated with the orchids was *Crematogaster* aff. *torosa,* found associated with three of the orchids studied in detail and three other species in the field. Table 2b presents a list of the ants found associated with orchids during field trips to areas near to sites 1 and 2.

General characteristics

The characteristics of the interaction between the various species of ants observed and the three species of *Encyclia* are presented in Table 3. The ants patrolled the mature flowers in all cases, and also the immature flowers of *E. chacaoensis* and *E. belizensis* var. *parviflora* and the buds of *E. cordigera* y *E. chacaoensis*. Feeding sites were more specific and for

Table 2a. Distribution of ant species among the five orchid species studied.

Ant species	*Encyclia chacaoensis*	*Encyclia cordigera*	*Encyclia belizensis* var. *parviflora*	*Catasetum integerrimum*	*Cycnoches ventricossum*
Crematogaster aff. *torosa*	x		x		x
Crematogaster sp. 2					
Monomorium floricola	x	x			
Cyphomyrmex rimosus	x				
Pseudomyrmex gracilis	x	x			
Pheidole gouldi		x		x	
Pheidole anastasii					x
Camponotus novogranadensis	x				
Camponotus elevatus	x				
Camponotus aff. *planatus*	x	x		x	
Camponotus aff. *guatemalensis*		x			
Camponotus sp. 2		x			

Table 2b. Ant species found associated with orchids in the field.

Crematogaster aff. *carinata*	*Cattleya skinneri*, *E. chacaoensis*, *Brassavola nodosa*
Crematogaster aff. *torosa*	*C. skinneri*, *Notylia barkeri, E. chacaoensis*
Crematogaster sp. 2	*B. nodosa*
Monomorium floricola	*B. nodosa*, *E. chacaoensis*, *E. cordigera*
Tapinoma melanocephalum	*E. chacaoensis*
Wasmannia auropunctata	*B. nodosa*
Dolichoderis debilis	*B. nodosa*
Pheidole gouldii	*C. integerrimum*
Solanopsis germinata	*N. barkeri*, *E. chacaoensis*
Camponotus novogranadensis	*N. barkeri*
Camponotus elevata	*C. aurantiaca* P.N. Don.
Camponotus sp. 1	*C. skinneri*

all species, much time was spent feeding at the base of mature flowers and at the union, or internodes between the petioles of adjacent flowers. The ants also scraped the general surface of the flower buds of *E. chacaoensis* and *E. cordigera* and fed from secretions produced at the immature flower tips of *E. belizensis* var. *parviflora* y *E. chacaoensis*. All three species of orchid showed visible signs of EFN production. *E. belizensis* var. *parviflora* was the only species which presented domatia, and on only one of the plants studied, in old, dry pseudobulbs, accessed by conspicuous holes near the base.

Ant behaviour

Camponotus novogranadensis was the only one of the seven species of ant associated with *E. chacaoensis* observed to be aggressive and to actively defend the plant; this ant recruited to the point where the plant was touched (Table 3). These seven species of ant were never found together on the same plant. The ants patrolling *E. cordigera* were passive and did not respond to disturbance (touching the plant), and visits were the least frequent of the three species. The ants that nested in the domatia on one of the plants of *E. belizensis* var. *parviflora* left their nest and fled the plant when it was touched, and clearly do not defend their host plant. No pests were present on the orchid plants at any time during the study, we could not, therefore, evaluate the value of ant presence in relation to herbivory.

Frequency of visits

Visits were most frequent to the EFNs of *E. belizensis* var. *parviflora* and peaked at 14.00hrs, with an average of 15 independent visits during the 5 min periods. Activity was reduced toward dusk, with 10.75 visits per 5 minute period at 18.00hrs. EFNs of *E. chacaoensis* and *E. cordigera* received a constant trickle of an average of 2.75 and 2.25 visits, respectively, per 5 min period during the whole day. It is clear from Fig. 1 that *E. belizensis* var. *parviflora* received the most visits during the study period, involving

Table 3. Characteristics of the interaction between ant visitors and three species of *Encyclia*.

	Encyclia chacaoensis	*Encyclia cordigera*	*Encyclia belizensis* var. *parviflora*
Reproductive structures visited	Buds, immature and mature flowers	Buds and mature flowers.	Immature and mature flowers
Feeding sites	General surface of buds, tip of immature flowers, mature flower bases, petiole junctions.	General surface of buds, mature flower bases, petiole junctions.	Tip of immature flowers, mature flower bases and stems, petiole junctions.
Presence of visible extrafloral nectar	Yes	Yes	Yes
Presence of domatia	-	-	In old, dry pseudobulbs
Behaviour when plant disturbed by touching	1 species aggressive 6 species passive	Passive	Escape
No. of species of ants present	7	7	1

only one species of ant. Most visits were observed at the time of peak flowering in April, with a sudden reduction in activity in June, when flowering ceased. In previous observations, in the field and in Site 1, the same species of ant was seen to continue patrolling plants of *E. belizensis* var. *parviflora* during the development and maturation of the seed capsules and to feed from secretions produced at the base of the withered flower. It is not clear why, in these observations, visits ceased at the end of the flowering period despite the presence of developing seed capsules. *E. chacaoensis* and *E. cordigera* show a different pattern of ant interaction, in which a similar level of ant activity on the plants was maintained at all times. These orchids flowered during March to May, after which the ants switched their attention to young shoots.

Discussion

Extrafloral nectaries produce secretions containing sugars (Baskin and Bliss, 1969) which attract the attention of ants and give rise to interactions of various intensities from casual, opportunistic visits to obligate mutualism; these interactions have been little studied in orchids. Most orchid species are notorious for offering no reward to pollinating insects, supposedly for reasons of resource economy in stressful environments. In that context, it is surprising to find that orchids invest scarce energy resources in the production of EFN to attract ants.

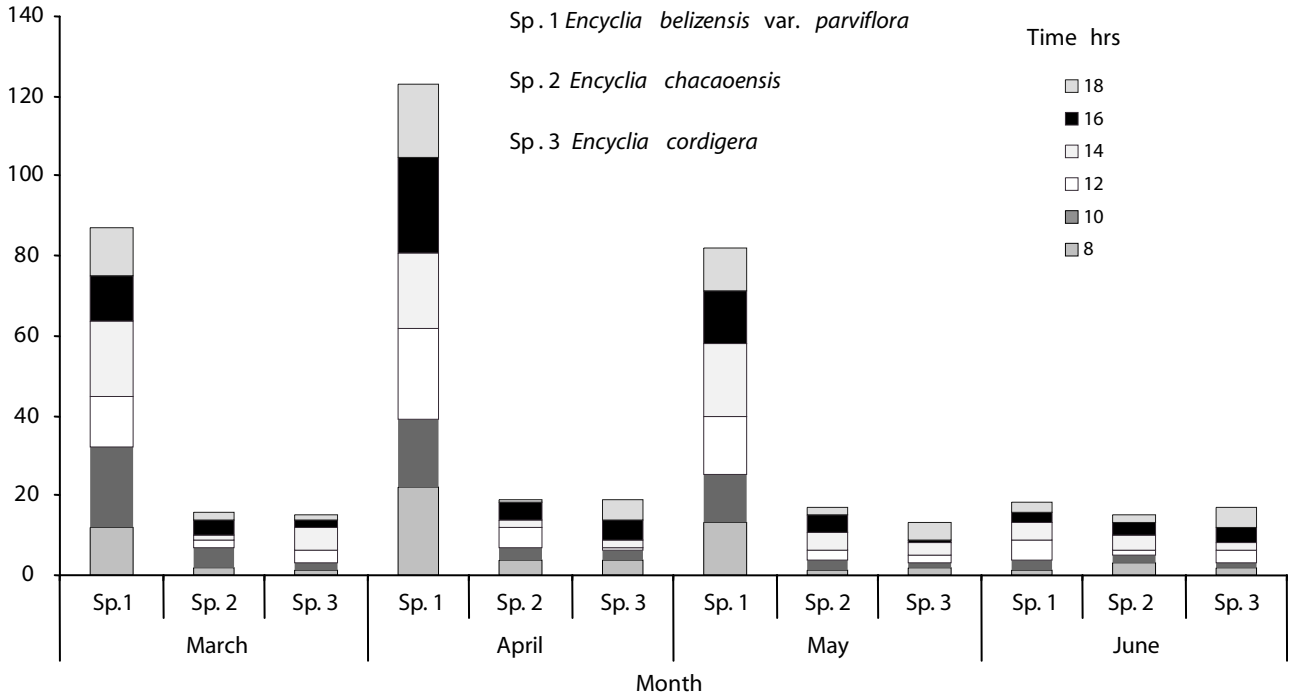
In the case of *E. belizensis* var. *parviflora*, *E. cordigera* and *E. chacaoensis*, well defined areas on flower bases and petiole junctions were visited by the ants. There was a greater frequency of ant visits to EFNs of *E. belizensis* var. *parviflora*, although by one species of ant only, *Crematogaster* aff. *torosa*, suggesting a degree of specialization towards a mutualistic interaction and this orchid species also offered refuge to the ants in the form of hollow, dry, old pseudobulbs, with access holes at the base. The benefit to the orchid, in this case, is likely to be alimentation via absorptive cells in the lining of the domatia, and not defense. The ant in question, *C.* aff. *torosa* was also found feeding upon the EFNs of other orchids in this study.

In general, the activities of these ant visitors may contribute towards the persistence of reproductive structures, without interfering with the pollination mechanism. Visits by pollinators for many species of orchid are rare and intermittent; it may benefit the plant to protect the flowers so that they persist for a greater period of time, increasing the likelihood of receiving a visit. However, in this study, pests were not a problem, so the contribution of patrolling ants as a defense strategy could not be evaluated. Furthermore, most of the ants observed were seen to be passive or neutral towards disturbance involving "their" plant, which does not suggest a defense role, except in the case *C. novogranadensis* associated with *E. chacaoensis.*

Further studies are required to see whether EFNs are present on immature flower tips and shoots, where ants were also seen to be feeding on occasion, or whether the ants are simple rasping and feeding on surface tissue. A comparative analysis of the content of the EFN produced at different times of day and at different phenological stages would be informative. However, the minute quantities of EFN produced would require the destructive sampling of many plants in order to obtain workable samples, which was not compatible with the aims of this study and the number of plants available.

Most of the ants collected in this study are common, amply distributed species, with many references to invasion of human dwellings and agroecosystems where they may be considered as pests (Klotz et al, 1995). Furthermore, most species are cited as generalized scavengers and frequent, opportunistic visitors to extrafloral nectaries. *Wasmannia*

Fig. 1. Relation between ant visits and time for three species of *Encyclia* in Soconusco Region.



auropunctata, given the name "little fire ant" is native to continental Central and South America and reported as a particularly aggressive and invasive species (Wetterer et al. 1999). Some species, such as *Crematogaster carinatus* and *C. torosus* are cited as arboreal species, abundant in mature, tropical rainforest canopies but also adaptable to seasonally dry areas, highly disturbed areas, and pasture edges (Longino, 2003). *C. carinatus* was cited as one of the dominant species in ant mosaics in Colombian rainforest and has been found sharing nests with *Dolichoderus debilis*, also found attending the EFN's of orchids in this study. *Cyphomyrmex rimosus* is a fungus growing species (Snelling and Longino, 1992). *Pseudomyrmex gracilis* associates with acacias (Cronin, 1998, Wetterer and Wetterer, 2003). *W. auropunctata*, *C. rimosus* and different species of *Pheidole* and *Dolichoderus* were found nesting in random association with tank bromeliads in the Venezuelan Amazonia (Blüthgen et al 2000).

This study presents evidence of encounters between opportunistic, foraging ants and 4 species of non myrmecophytic orchids, *E. chacaoensis*, *E. cordigera*, *C. integerrimum* and *C. ventricosum*. Interaction between *E. belizensis* var. *parviflora* and *Crematogaster* aff. *torosa* may be more specific and this orchid may be considered as a mymecophyte. However, there was no evidence to suggest that this orchid benefited from reduced herbivory during the study period but is likely that the resident ants provide organic matter for the plant.

The most important question arising from this study is why do resource-constrained orchids produce EFN, that is attractive only to ants, when there is minimal likelihood of pest attack and the ants attracted are mostly non-aggressive and would not, in any case, repel insect pests? The study was carried at the beginning of the rainy season, humidity was not particularly high (max. 55% at 16.00hrs) so passive excretion, thought to be the evolutional origin of sweet, watery secretions by plants, was not an acceptable explanation. It is possible that the original target of these EFNs were other species of ants present in undisturbed tropical humid forests, which did play a defensive role and that in highly disturbed environments the specialized interactions may break down or become obsolete. The author is also finding that increasingly rare pollination events in orchids in Soconusco are being carried out by a few, common and generalist pollinators (Damon, unpublished). The interaction clearly lacks a feedback mechanism or synchrony between the two organisms (Hölldobler and Wilson 1990) and resource limited plants continue to secrete extrafloral nectar despite the presence of unrewarding, opportunistic ant species which may, therefore be considered as nectar robbers.

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