

Interhabitat differences in ant activity on plant foliage: ants at extrafloral nectaries of *Hibiscus pernambucensis* in sandy and mangrove forests

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Abstract

The association between visiting ants and the extrafloral nectaries (EFN)-bearing shrub *Hibiscus pernambucensis* Arruda (Malvaceae) was investigated in two different coastal habitats – a permanently dry sandy forest and a regularly inundated mangrove forest. In both habitats the frequency of plants with ants and the mean number of ants per plant were much higher on *H. pernambucensis* than on non-nectariferous neighbouring plants. In the sandy forest the proportion of live termite baits attacked by ants on *H. pernambucensis* was much higher than on plants lacking EFNs. In the mangrove, however, ants attacked equal numbers of termites on either plant class. Ant attendance to tuna/honey baits revealed that overall ant activity in the sandy forest is higher than in the mangrove area. The vertical distribution (ground vs. foliage) of ant activity also differed between habitats. While in the mangrove foraging ants were more frequent at baits placed on foliage, in the sandy forest ant attendance was higher at ground baits. Plants housing ant colonies were more common in the mangrove than in the sandy forest. Frequent flooding in the mangrove may have resulted in increased numbers of ant nests on vegetation and scattered ant activity across plant foliage, irrespective of possession of EFNs. Thus plants with EFNs in the mangrove may not experience increased ant aggression towards potential herbivores relative to plants lacking EFNs. The study suggests that the vertical distribution of ant activity, as related to different nest site distribution (ground vs. foliage) through a spatial scale, can mediate ant foraging patterns on plant foliage and probably affect the ants' potential for herbivore deterrence on an EFN-bearing plant species.

Introduction

Ants are social insects that occur in virtually all types of habitats and whose colonies may occupy a multitude of nest sites, ranging from terrestrial to arboreal nests (Hölldobler & Wilson, 1990). In the tropics a great number of ant species forage intensively on plant foliage, where they search for arthropod prey, plant-derived food products, as well as liquid rewards secreted by insect herbivores (Carroll & Janzen, 1973; Oliveira et al., 2002). While food resources occurring on foliage are probably easier to find and exploit by arboreal nesting species

(Wilson, 1987; Davidson, 1997), many ground-nesting ants also extend their foraging areas by searching for food on the plant substrate (Way, 1963; Bentley, 1977; DeVries, 1991; Del-Claro & Oliveira, 1999). Extrafloral nectaries (EFNs) represent one of the main predictable food sources found on tropical foliage, and ants are by far the most frequent visitors to these glands (Carroll & Janzen, 1973; Bentley, 1977; Oliveira & Brandão, 1991). By exhibiting aggressive behaviour towards herbivores, EFN-gathering ants can positively affect plant fitness by decreasing herbivore damage to leaves (Koptur, 1979; Smiley, 1985), buds or flowers (Rico Gray & Thien, 1989; Oliveira, 1997), and seeds (Inouye & Taylor, 1979; Keeler, 1981). In some cases, however, visiting ants apparently do not benefit the plant (e.g., Whalen & MacKay, 1988). In fact the outcomes of such facultative ant–plant mutualisms may vary with factors

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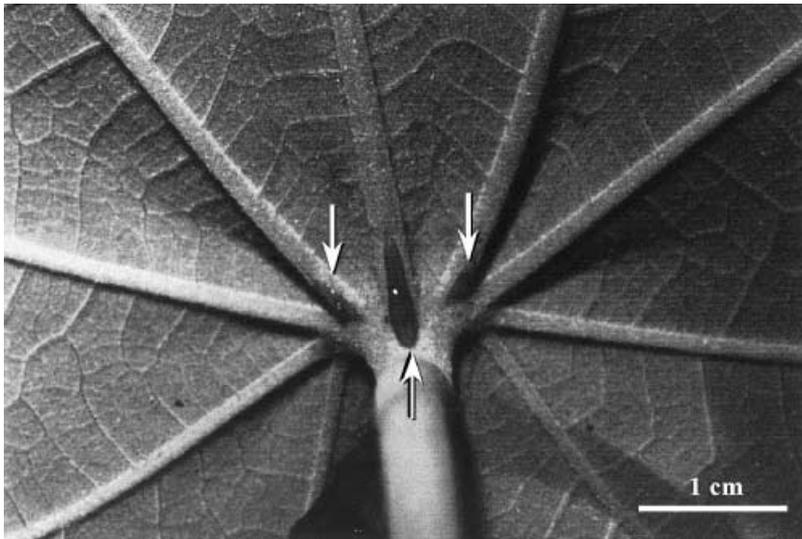


Figure 1 Extrafloral nectaries (arrows) on the under-leaf surface of *Hibiscus pernambucensis*.

such as time, habitat type, ant species, rate of ant visitation, as well as with the capacity of herbivores to overcome ant predation (see Koptur, 1992; Bronstein, 1998; De la Fuente & Marquis, 1999; Oliveira et al., 1999, and references therein).

Several factors can account for the spatial variation in ant-derived benefits to EFN-bearing plants. These may include proximity to ant nests (Inouye & Taylor, 1979), among-site variation in the abundance of ants and herbivores (Barton, 1986), spatial heterogeneity in ant constancy at plants (Smiley, 1986), among-site differences in ant communities (Horvitz & Schemske, 1984), and variable ant-derived protection between sun and shade microhabitats (De la Fuente & Marquis, 1999).

In the present paper we focus on the association between visiting ants and the EFN-bearing shrub *Hibiscus pernambucensis* Arruda (Malvaceae). This species has three slender EFNs on the under-leaf surface, near the petiole insertion (Figure 1; Rocha & Neves, 2000; Cogni & Freitas, 2002). *Hibiscus pernambucensis* is native to coastal areas of Bermuda, southern Florida, the Bahamas, the Greater and Lesser Antilles, and from Mexico to the Atlantic and Pacific coastal habitats of South America (Francis, 2002). This ant–plant system offers a unique opportunity to investigate spatial variation of ant visitation patterns, because the plant grows on two quite different coastal habitats – a permanently dry sandy forest and a regularly inundated mangrove forest. Four questions were addressed: (1) Do EFNs increase ant visitation to *H. pernambucensis* over that of non-nectariferous vegetation? (2) Do ants attack potential herbivores on leaves, and is aggression more frequent on *H. pernambucensis* than on non-nectariferous plants? (3) Are ant visitation rates and ant aggressiveness different between habitats? and (4) Can differences in

ant visitation and aggression be explained by differences in the vertical distribution (ground vs. foliage) of ant activity and nest sites between the two habitats?

Materials and methods

Fieldwork was carried out at the Parque Estadual da Serra do Mar, in Ubatuba (44°55'W; 23°20'S), state of São Paulo, south-east coast of Brazil. The climate is generally warm and wet, with a mean annual temperature of 21.4 °C and annual rainfall of 3160 mm. Shrubs of *H. pernambucensis* were studied in two types of coastal habitats – mangrove and sandy forest. Located in the mouth of the Picinguaba River, the mangrove site is flooded twice a day during semidiurnal high tide. During flooding the water level reaches nearly 30 cm above ground. Principal plant species in the mangrove site include *Rhizophora mangle* (Rhizophoraceae), *Avicennia schaueriana* (Verbenaceae), *Laguncularia racemosa* (Combretaceae), the fern *Acrosticum aureum*, and *H. pernambucensis* (Alonso, 1977). The sandy forest is 200 m from the sea and is not flooded. This forest has an open canopy formed by 5–15 m tall trees growing on poor sandy soil (Barros et al., 1991), with *Schinus terebinthifolius* (Anacardiaceae), *Clusia criuva* (Clusiaceae), *Erythrina speciosa* (Leguminosae), and *H. pernambucensis* among the most common plant species. The study sites are 3.5 km apart, and *H. pernambucensis* occurs at a density of ca. 30–50 individuals along a 100-m transect in either habitat. Fieldwork was undertaken during the wet and warm season, January–April 2000 and 2001.

The pattern of ant foraging on the vegetation was evaluated by tagging 60 experimental plant pairs in either habitat. Each pair consisted of a shrub of *H. pernambucensis*

(1–2.5 m tall) and the nearest similar-sized plant without EFNs (plants hosting honeydew-producing homopterans were not used because they may have similar ecological functions; see Messina, 1981; Koptur, 1992). This method is frequently used to evaluate ant visitation to EFN-bearing plants (e.g., Oliveira et al., 1987; Oliveira, 1997). The principal plants used as the nearest neighbour were *Avicennia schaueriana* and *Laguncularia racemosa* in the mangrove forest, and *Clusia criuva* and *Schinus terebinthifolius* in the sandy forest. To see whether EFNs increased ant visitation to *H. pernambucensis* over that of non-nectariferous plants, the number of ant foragers on each plant of a pair was counted upon our arrival. The behaviour of foraging ants towards potential herbivores was evaluated by using live workers of termites (*Nasutitermes*) as baits (simulated herbivores) on experimental plants. Live insect baits have already been used in the field to evaluate patterns of ant predation (Barton, 1986; Freitas & Oliveira, 1996). Live termites were glued by the dorsum (legs upwards) on the centre of the leaf blade with a fast-drying adhesive (Tenax®, Loctite Brazil Ltd). The adhesive had no apparent effect on ant behaviour. One termite was placed simultaneously on a leaf of each plant of an experimental pair ($n = 60$ pairs in each site). Attacks on termites by foraging ants were recorded for both plants of a pair within a 60-min period. To search for differences in discovery time of termites by foraging ants, 60 additional experimental plant pairs were tagged in each site. Using the same baiting procedure described above, we recorded the discovery time by ants during a 10-min period for both plants of a pair. Calculation of discovery time included only termites discovered by ants. All ant censuses and baiting experiments were carried out during sunny days (07.00–16.00 hours), and a given plant pair was used only once.

To search for differences in the vertical distribution (ground vs. foliage) of ant activity in the mangrove and in the sandy forest, we attracted ants by placing tuna/honey baits on the ground and on vegetation (plants within 1–2.5 m height). Each bait consisted of a 0.5-cm pellet of tuna and two droplets of honey placed on a 5×5 cm filter paper. In each site 50 baits were distributed (3 m apart) on either foraging substrate along part of a 300-m transect (total 100 baits per habitat). Baiting on the ground and on vegetation was performed on different days. On each substrate, baits were all placed at the same time. Ant occurrence at baits was checked after 30 min. In the mangrove, ground baits were placed 5 h after flooding. The nest location of the ant species attracted to baits was determined by following loaded returning ants (any additional ant colony not recruiting to baits was not detected by this method). Baiting and behavioural observations were carried out on sunny days (07.00–16.00 hours). Ant voucher specimens

are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil.

To search for interhabitat differences in soil conditions (softness) that could potentially affect the construction and maintenance of ant nests on the ground, we evaluated soil softness in mangrove and sandy forest along a 100-m transect in each area. We released a sharpened wire stake (50 cm long) from the inside top of a 1.5-m high plastic PVC tube. The depth reached by the stake into the ground was used to estimate soil softness for each habitat (Passos & Oliveira, 2001). In the mangrove, soil condition was evaluated 5 h after flooding.

Results

In the mangrove forest, the proportion of *H. pernambucensis* plants occupied by ants greatly surpassed that of neighbouring plants without EFNs ($P = 0.002$; G-test; Figure 2A). The average number of ants on *H. pernambucensis* was also higher than on non-nectariferous plants ($P < 0.005$; Wilcoxon paired-sample test; Figure 2C). The proportion of termite baits attacked by foraging ants, however, did not differ between the two groups of plants ($P = 0.26$; G-test; Figure 2E). Termites were discovered at equal times on either plant class (mean \pm SD_{Hibiscus} = 3.6 ± 2.9 min, $n = 24$; mean \pm SD_{neighbour} = 4.6 ± 2.9 min, $n = 16$; $P = 0.30$; Mann–Whitney U-test).

In the sandy forest, both the frequency of ant occupancy ($P < 0.0001$; G-test) and mean number of ants per plant ($P < 0.001$; Wilcoxon paired-sample test) were also much higher on *H. pernambucensis* than on non-nectariferous plants (Figure 2B,D). As opposed to the mangrove site, however, in the sandy forest the proportion of termites attacked by ants on *H. pernambucensis* was much higher than on plants lacking EFNs ($P < 0.01$; G-test; Figure 2F). Discovery time of termites by foraging ants did not differ between plant classes in the sandy site (mean \pm SD_{Hibiscus} = 3.7 ± 2.6 min, $n = 22$; mean \pm SD_{neighbour} = 4.1 ± 2.7 min, $n = 11$; $P = 0.59$; Mann–Whitney U-test).

The data on ant attendance to tuna/honey baits revealed that overall ant activity in the sandy forest is higher than in the mangrove area (71% vs. 44% of baits discovered by ants; $P < 0.001$; G-test; Figure 3). The vertical distribution (ground vs. foliage) of ant activity also differed markedly between habitats. While in the mangrove forest foraging ants were more frequent at baits placed on foliage, in the sandy forest ant attendance was higher at baits placed on the ground ($P < 0.0001$, G-tests; Figure 3). The species composition of the ant assemblages attending the baits in both habitat types is shown in Table 1. In the mangrove forest (seven species) an arboreal *Camponotus* species attended 50% of the baits placed on leaves. In the sandy forest (nine species) a ground-nesting *Linepithema* species

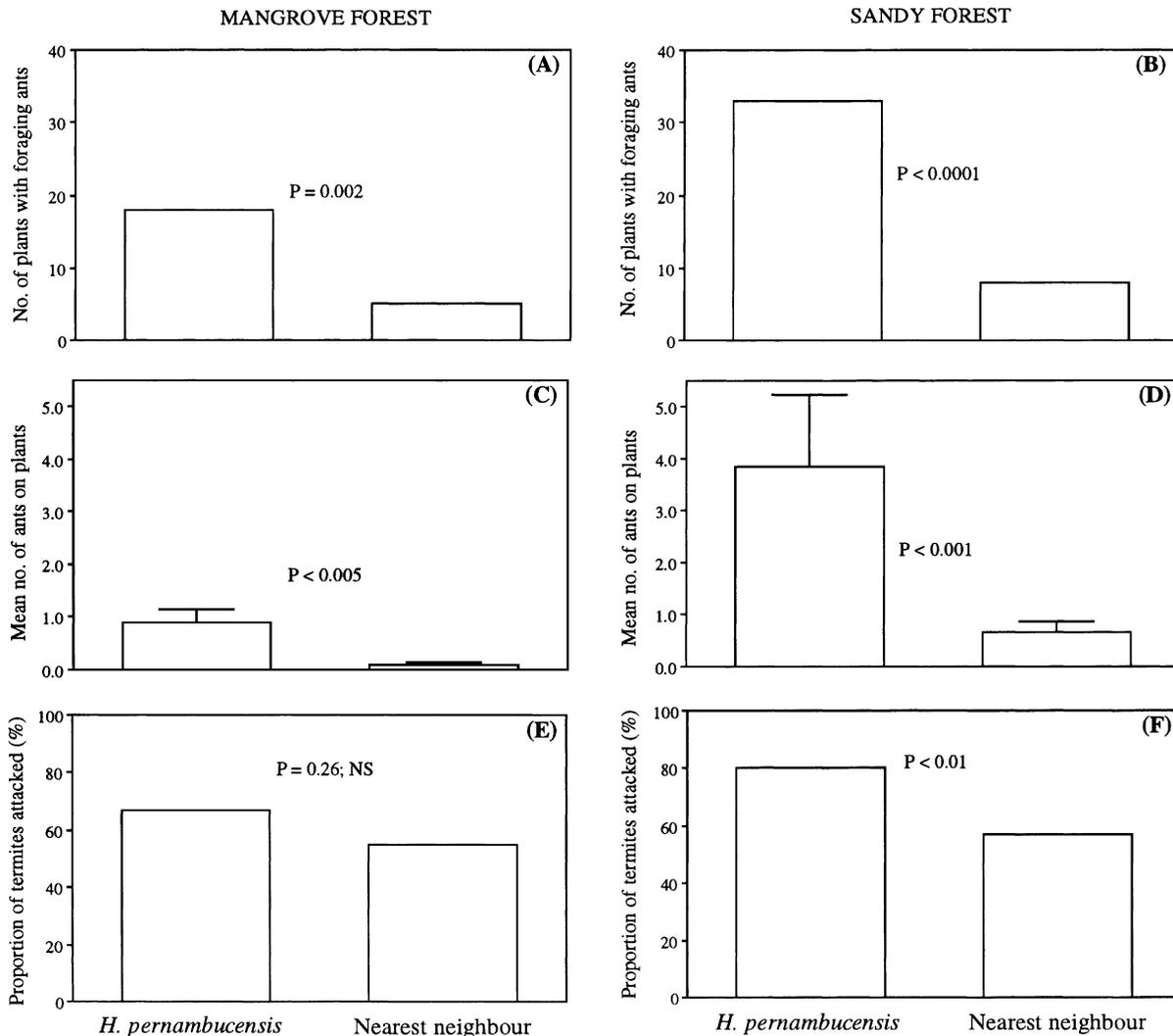


Figure 2 Ant occupation of plants in mangrove and sandy forest habitats on the coast of south-east Brazil. Data were gathered on EFN-bearing *Hibiscus pernambucensis* and on nearest neighbours lacking EFN ($n = 60$ for each class). (A, B) Number of plants occupied by ants. (C, D) Mean number of ants on plants. Vertical bars show standard error. (E, F) Proportion of termite baits attacked by ants on foliage (one termite per plant of a pair). NS = not significant.

accounted for 78% of the ground baits. The proportion of plants housing ant colonies (based on loaded returning ants) in the mangrove environment was higher than in the sandy forest ($P < 0.001$; G-test; Figure 3). Due to intense flooding and higher softness of the soil in the mangrove forest, the wire stake penetrated significantly deeper into the ground in this area (13.4 ± 2.5 cm) than in the sandy forest (8.1 ± 1.5 cm; $P < 0.0001$; Mann–Whitney U-test).

Discussion

Many studies in temperate and tropical ecosystems have demonstrated that the presence of EFNs increases ant

density on the plant, and that the ants' aggressive behaviour on foliage deter associated herbivores (Barton, 1986; Oliveira et al., 1987; Koptur, 1992, and references therein). Our results show that possession of EFNs increases ant density on *H. pernambucensis* over that of non-nectariferous plants both in mangrove and sandy forests. Only in the sandy forest habitat, however, does ant visitation of an EFN-bearing plant result in a higher proportion of termite baits attacked by ants relative to the background vegetation that lacks EFNs. In the mangrove forest termites were attacked in equal numbers on either type of plant. These results suggest that the potential antiherbivore activity of ants may only manifest itself as a

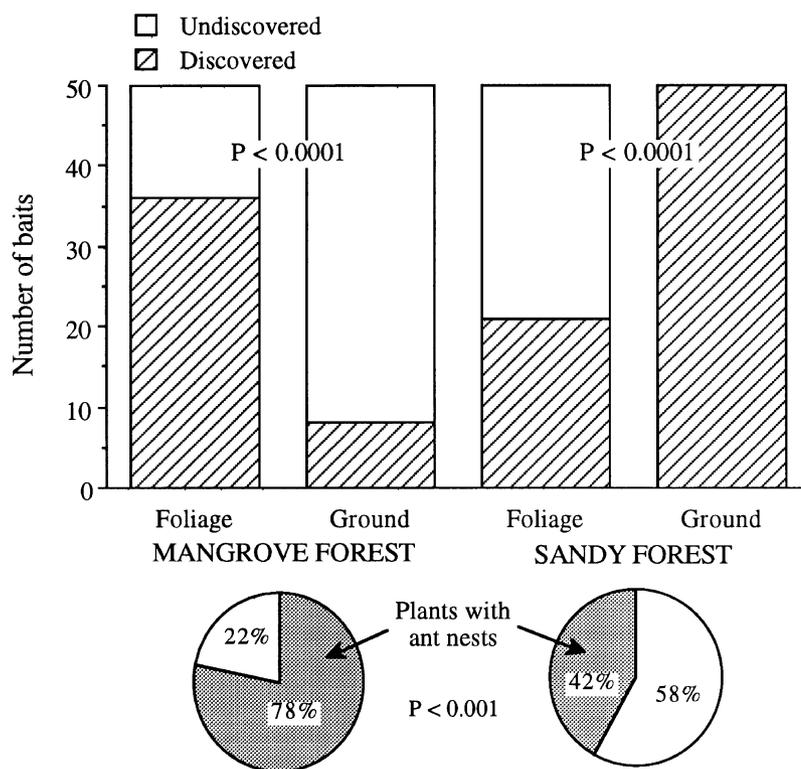


Figure 3 Ant attendance to honey/tuna baits placed on vegetation ($n = 50$) and on the ground ($n = 50$) of mangrove and sandy forest habitats on the coast of south-east Brazil. Data indicate that the proportion of baits discovered in either substrate depends on the habitat. The hatched area in the lower pie charts indicates the proportion of plants housing ant colonies in mangrove and sandy forest (total 50 plants checked in each habitat).

benefit of EFNs in particular habitats (see also Barton, 1986).

Differences in the proportion of termites attacked by ants in the two areas are probably due to low ant activity in the mangrove. Both ant visitation to plants (Figure 2) and overall attendance to baits (Figure 3) were lower in the mangrove than in the sandy forest. A similar pattern was observed in Australia, where the discovery of baits by ants

was much lower in mangrove forest than in nearby savannas (Clay & Andersen, 1996). Low ant activity in mangrove ecosystems may be caused by several factors. First, daily flooding makes the sediment too soft and moist, resulting in unsuitable conditions for ant nests. In fact, our data using the wire stake show that the soil in the mangrove area was much softer than in the sandy forest. Although a few specialist ants, such as *Polyrhachis sokolova*, are reported to

Table 1 Number of baits (tuna and honey) found by each ant species on the ground and at vegetation in sandy and mangrove forest in Picinguaba, south-east Brazil. V = nest at vegetation, G = nest on the ground

Ant species	Nest	Sand Forest		Mangrove	
		Ground	Vegetation	Ground	Vegetation
DOLICHODERINAE					
<i>Linepithema</i> spec.	G	34	1	4	1
FORMICINAE					
<i>Brachymyrmex</i> spec. 2	V	1	4	–	–
<i>Camponotus crassus</i> Mayr	V	2	–	–	–
<i>Camponotus</i> spec. 2	V	3	1	1	25
MYRMICINAE					
<i>Cyphomyrmex</i> spec.	G	3	–	–	–
<i>Crematogaster</i> spec.	V	–	1	–	4
<i>Leptothorax</i> spec.	G,V	1	1	–	–
<i>Pheidole</i> spec.	G	–	–	3	–
<i>Solenopsis</i> spec. 2	V	7	8	–	5
PSEUDOMYRMECINAE					
<i>Pseudomyrmex gracilis</i> (Fabricius)	V	10	5	–	4
<i>Pseudomyrmex kuenckeli</i> (Emery)	V	–	–	–	1

nest in intertidal mud in Australian mangrove (Nielsen, 1997), the extreme conditions of this environment limit the presence of almost all ground nesting ant species (Clay & Andersen, 1996; Cogni & Freitas, 2002). Second, crabs are extremely abundant ground scavengers in mangroves and may be involved in competitive interactions with ants (Clay & Andersen, 1996).

The only way foraging ants can reach plant foliage when the mangrove ground is flooded (water level \approx 30 cm above ground) is by bridges formed by branches and fallen wood. Indeed, the importance of connecting bridges for increasing both ant density and ant species richness on EFN-bearing plants has been shown for other tropical ecosystems (Schemske, 1982; Apple & Feener, 2001). In mangrove environments, due to regular flooding, the presence of bridges can markedly affect ant activity on plants. In a study in Indonesia, Ozaki et al. (2000) have shown that in natural mangrove forest, where there are bridges connecting plants, ant predation suppresses populations of scale insects. On the other hand, in artificial plantations without between-plant bridges, ants are unable to reach the plants and scale insect outbreaks are common (Ozaki et al., 2000). It is possible that the extensive use of plants as bridges in the mangrove may have partially accounted for the similar antiherbivore behaviour of ants on nectariferous and non-nectariferous plants in this habitat.

Another interesting peculiarity of ant distribution in this habitat is the predominance of arboreal species (Nielsen, 2000). As opposed to the sandy forest, in the mangrove area many more baits were discovered by ants on the vegetation than on the ground (Figure 3). A similar pattern was observed in Australian mangroves (Clay & Andersen, 1996). Additionally, plants housing ant nests were much more frequent in the mangrove than in the sandy forest (Figure 3). Ants are known to behave aggressively towards intruders in the vicinity of the nest and near a food source, and this is referred to as 'ownership behaviour' (Way, 1963). Thus, a large proportion of plants housing ant nests in the mangrove possibly makes ant aggression due to ownership behaviour more scattered across plant foliage (including plants without EFNs) in this habitat than in the nearby sandy forest. In the latter area, possession of EFNs by *H. pernambucensis* apparently results in increased ant aggression on this plant compared to neighbouring plants lacking EFNs.

Interhabitat differences in ant visitation patterns to EFNs have already been recorded in ant-plant systems of other regions, resulting in spatial variation in ant-derived benefits to EFN-bearing plants (e.g., Bentley, 1976; Barton, 1986). Interhabitat variation in the outcome of ant-plant systems mediated by EFNs are usually caused by differences in the species composition of the associated ant

community, variable herbivore pressure, or variable ant density on foliage (Bentley, 1976; Horvitz & Schemske, 1984; Barton, 1986; Smiley, 1986; De la Fuente & Marquis, 1999). The current study suggests that the vertical distribution of ant activity, as related to different nest site distribution (ground vs. foliage) through a spatial scale, can mediate ant foraging patterns on plant foliage and probably affects the ants' potential for herbivore deterrence on a EFN-bearing plant species.

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