Ants and plant size shape the structure of the arthropod community of *Hirtella myrmecophila*, an Amazonian ant-plant

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Abstract. 1. To investigate the influence of plant size and the presence of resident ants on the arthropod community associated with the ant-plant *Hirtella myrmecophila*, ants (*Allomerus octoarticulatus*) were experimentally removed from plants of various sizes, with a second group of similar-sized plants remaining as controls. The abundance and diversity of arthropods on these plants were determined at 45-day intervals for 7 months. Collected arthropods were assigned into one of three predetermined groups: herbivores, spiders (mostly web-building spiders), or 'tourists' (mostly non-resident ants, hemipterans, dipterans, or scarabeid beetles).

2. Ant removal had a positive influence on the abundance and diversity of herbivores, but no measurable effects on the abundance and diversity of 'tourists', while the effect on spider abundance was significant only when data from *Dipoena* sp. nov. were removed from the analysis. While *A. octoarticulatus* had a negative effect on most spiders, it favoured *Dipoena* sp. nov., which was found to be a specialist predator of *A. octoarticulatus*.

3. Plant size positively affected the abundance and diversity of 'tourists' in plants with and without ants, but for herbivores and spiders this effect was dependent on ant treatment. In ant-maintained plants the per-plant abundance of herbivores and spiders was independent of plant size, whereas in ant-removed plants it was not.

4. These results suggest that *A. octoarticulatus* affects all arthropods found on its host plant, except those presenting an occasional and temporary association with the plant, and that the magnitude of ant effects on the susceptible guilds increases as plant size increases.

Key words. *Allomerus*, ant–plant interactions, biotic defences, community structure, *Dipoena*, keystone predators, plant ontogeny, mutualisms, spiders.

Introduction

Ants are a keystone group in most terrestrial ecosystems (Hölldobler & Wilson, 1990). They are extremely abundant,

diverse, and can occupy more than one trophic level in a community. Furthermore, as eusocial insects, ants have behavioural strategies that allow them to capture prey several times their own size, and defend the nest and its vicinity against enemies (Hölldobler & Wilson, 1990). These characteristics have perhaps facilitated the evolution in various tropical angiosperms of specialised structures, also known as domatia, that allow the temporary or permanent association of ants with plants (Benson, 1985; Davidson & McKey, 1993). In addition to nesting space,

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myrmecophytes often also provide food (food bodies and/ or extrafloral nectar) to their associated ants, and in exchange receive protection against herbivores (Janzen, 1966; Beattie, 1985; Vasconcelos, 1991; Fonseca, 1994; Heil *et al.*, 2001), against encroaching vines (Davidson & McKey, 1993; Federle *et al.*, 1998; Suarez *et al.*, 1998), or receive nutrients from decaying ant nest debris (Janzen, 1974; Treseder *et al.*, 1995). In general, ants associated with myrmecophytes do not nest elsewhere but in a restricted number of myrmecophytic species (Benson, 1985; Fonseca & Ganade, 1996).

It is well established that, given their predatory behaviour, plant-ants frequently reduce herbivore abundance, and consequently herbivory in their myrmecophytic host plants (e.g. Janzen, 1966; Vasconcelos, 1991; Fonseca, 1994). However, not only herbivores, but also a variety of other organisms, especially arthropods, can establish relationships with plants, from sporadic and non-specific relationships to more permanent and specific ones (Strong *et al.*, 1984). Many web-building spiders, for instance, establish their webs on myrmecophytes (Venticinque & Fowler, 1996), but the impact of ants on these organisms, and other non-herbivore arthropod guilds, is poorly known. Also, few studies have looked at the effects of plant structure on the composition of arthropod communities living on myrmecophytes, in spite of its known effects on non-myrmecophytes (Strong *et al.*, 1984).

Here, it was examined how plant size and the presence of mutualistic ants interact in determining the composition of the arthropod community of an ant-plant. An experimental approach was used to determine how arthropod abundance and diversity respond to ant presence and to variations in host-plant size, and to determine if these effects were similar for different guilds of arthropods. For this, the obligate association between *Hirtella myrmecophila* (Chrysobalanaceae) and its main ant associate *Allomerus octoarticulatus* (Izzo & Vasconcelos, 2002) was studied. *Hirtella myrmecophila* is a small (<8 m) understorey tree commonly found in non-flooded forests of central Amazonia, and that produces leaf pouches as domatia. *Allomerus octoarticulatus* is a tiny ant (<2 mm), a relative of the fire ants, that lives exclusively in myrmecophytes (Izzo & Vasconcelos, 2002). *Hirtella myrmecophila* drops domatia from older leaves – a characteristic that is unique among myrmecophytes and that allows for the existence, within the same plant, of branches with and without ants. Older branches generally bear only old leaves with no domatia, and therefore have no ants, whereas young branches have leaves of various ages (Izzo & Vasconcelos, 2002).

Materials and methods

Study area

The study was conducted at 'camp 41', an 800-ha forest reserve run by the Biological Dynamics of Forest Fragments Project (a collaborative project between INPA – the Brazilian National Research Institute for the Amazon – and the Smithsonian Institution). This reserve is situated about 70 km north of Manaus (2°25′S, 59°48′W), within an area of approximately 500 000 ha of relatively undisturbed, upland (*terra firme*) Amazonian rainforest that is being developed by the Manaus Free-Trade Zone Authority (SUFRAMA). The reserve is on moderately rugged terrain, dissected by small creeks, and lies at an elevation of 50–100 m. Canopy height of forest trees is about 35 m, with some emergent trees reaching up to 50 m. The understorey is relatively open and characterised by an abundance of stemless palms. Precipitation in Manaus averages 2100 mm annually and varies seasonally, with a rainy period between November and May and a dry period between June and October (Ribeiro, 1976). For more information about the study area see Bierregaard *et al.* (2002).

Sampling design

Within an area of about 300 ha, 34 individual of *H. myrmecophila* plants, 1–2.25 m in height, were selected. This size was chosen in order to facilitate the access to the plant canopy with minimal disturbance. As plant selection was made at random, selected plants were located within a relatively wide range of topographic and light conditions, although none of them was located in canopy gaps (where *H. myrmecophila* is almost absent). The minimum distance between any two plants was about 70 m whereas the maximum was 2 km. The total number of leaves and the number of secondary branches was determined for each plant. The number of leaves was used here as a measure of plant size, and as plants with more leaves had significantly more branches ($r = 0.757$, $P < 0001$) then numbers of leaves also represent the plant's structural complexity.

Selected plants were then assigned into two treatments: 19 into the experimental group (ants removed), and 15 into the control group (ants maintained). Ants were removed by applying 1 ml of a 1% aqueous solution of the organophosphate insecticide Malathion® (Indol do Brazil, Curitiba, P.R.) in each domatium present in the plant. The contact insecticide used here has a very short residual time and thus does not affect the colonisation of herbivores in ant-removed plants, as already shown in previous experiments (Vasconcelos, 1991). At the beginning of the experiment, there was no difference in the number of leaves ($t_{32} = -0.545$, $P = 0.589$) or in the number of branches ($t_{32} = -0.452$, $P = 0.654$) between control and experimental plants.

Starting 45 days after the beginning of the experiment, and thereafter every 45 days for 7 months, all arthropods seen on the plant surface were collected. The collection was made using tweezers and an aspirator, with extreme care to promote the smallest possible disturbance to the plant, avoiding direct contact with the leaves or branches. In each collection event the researcher first stayed for at least 1 h observing the behaviour of the arthropods seen on the

plant. The collected specimens were sorted into morphospecies (except for spiders, given the inherent difficulties in identifying the juveniles) and assigned into one of three predetermined arthropod groups: (1) herbivores, (2) 'tourists', or (3) spiders. Only species actually seen feeding on the plant were classified as herbivores. The 'tourists' group included mostly saprophagous, polinivorous, or predatory species that clearly did not live on the plant, or had an observable trophic relation with the plant, and therefore were just 'passing by'. In contrast, most spiders were web-building spiders (Araneidae and Theridiidae), which therefore live on the plant. Similarly, many hunting spiders, especially Salticidae, were found nesting on plant parts, and therefore clearly had a more permanent association with *H. myrmecophila* than any other arthropod classified as 'tourist'.

Statistical analysis

The total abundance of arthropods in each plant was determined by summing up the results of the five sampling events, whereas the cumulative number of morphospecies found represented species richness. Each arthropod group was analysed separately using analysis of covariance (ANCOVA). The effects of plant size, experimental treatment (with ants or ants removed), and the interaction between these two factors were tested. The mean number of leaves, calculated as: (initial number of leaves + number of leaves 7 months later)/2, was used as a measure of plant size. When a significant interaction between plant size and treatment was detected, *post hoc* linear regressions were conducted in order to separately analyse the effect of plant size for plants with or without ants. In this case, resulting probabilities were corrected using the Bonferroni procedure in order to account for the fact that the same hypothesis was tested twice (Benjamini & Hochberg, 1995). In addition, a *t*-test was used to test for the effects of the experimental treatment, independently of the effects of plant size. All analyses were carried out using SYSTAT 8.0 (Wilkinson, 1996).

Results

The most common arthropods classified as 'tourists' included ants (other than *A. octoarticulatus*), reduvid hemipterans, scarabeid beetles, and dipterans. The results of the ANCOVA indicated a significant and positive effect of plant size on both the abundance and species richness of 'tourists', but no effect of the ant removal treatment (Table 1, Fig. 1). There was no significant interaction between the effects of plant size and ant removal on the abundance and species richness of 'tourists'.

In contrast, a significant interaction between ant effects and plant size effects on the richness and abundance of herbivores was detected (Table 1), indicating that these two factors could not be analysed simultaneously.

Subsequent analyses showed that removal of ants significantly increased the abundance ($t_{32} = 2.26$, $P = 0.021$) and species richness ($t_{32} = 3.23$, $P = 0.003$) of herbivores. In plants without *Allomerus*, both the abundance and species richness of herbivores increased as plant size increased (abundance: $R^2 = 0.389$, $F_{1,17} = 10.80$, $P = 0.004$; species richness: $R^2 = 0.456$, $F_{1,17} = 14.27$, $P = 0.002$), while for ant-maintained plants no effect of plant size was detected (abundance: $R^2 = 0.045$, $F_{1,13} = 0.62$, $P = 0.446$; species richness: $R^2 = 0.002$, $F_{1,13} = 0.02$, $P = 0.883$).

The greater abundance of herbivores in ant-removed plants was partly due to the presence of the adults of two unidentified species of chrysomelid beetles, who were almost absent from ant-maintained plants. Both species apparently only feed on young leaves, generally consuming the entire leaf, and promoting serious damages to the plant. Other common herbivores on *H. myrmecophila* included two species of bruchid beetles, two species of Lepidoptera larvae, and one acridid treehopper. In plants with ants, these five morphospecies were found feeding mainly on mature and old leaves, although in ant-removed plants they also fed on young leaves.

For spiders, results of the ANCOVA indicated no significant effect of plant size and no effect of the ant exclusion treatment (and no interaction between these two factors) on the overall abundance of spiders (ANCOVA, $P > 0.05$ in all cases). However, these data were further analysed by excluding *Dipoena* sp. nov. (Theridiidae) individuals, because its feeding habits contrast sharply with all remaining spiders found on *H. myrmecophila*. While the latter appear to be generalist predators, it was found that *Dipoena* sp. nov. feeds only on *A. octoarticulatus*. In total (including observations on plants not marked for the present study), more than 200 *Dipoena* sp. nov. individuals were observed, and during over 32 incidents of prey capture, only workers of *A. octoarticulatus* were attacked. *Dipoena* sp. nov. establishes its web near the domatium entrance, and attracts its ant prey by vibrating the leaf surface. When the ant falls from the leaf or otherwise touches the web, it is attacked and immediately wrapped in silk for later consumption. This spider was commonly found in plants with *Allomerus* (up to 21 individuals were found in a single plant; mean of 3.3 spiders per plant), but in ant-removed plants only two individuals were found. Furthermore, in ant-inhabited plants the abundance of *Dipoena* sp. nov. was positively related to plant size ($R^2 = 0.58$, $F_{1,33} = 45.5$, $P < 0001$).

When data on *Dipoena* sp. nov. was excluded, then a significant interaction between the effects of plant size and ant-removal treatment on the abundance of spiders was detected (Table 1). Therefore, as was done with data on herbivores, these two factors were then analysed separately. The analysis for the effect of ant exclusion indicates that significantly more spiders were found in ant-excluded plants than in control plants ($t_{32} = 2.77$, $P = 0.009$). In the former, a positive relationship was found between plant size and spider abundance ($R^2 = 0.298$, $F_{1,17} = 7.23$, $P = 0.016$), while in ant-maintained plants the abundance

Table 1. ANCOVA summary statistics for the effects of plant size and ants (with ants or ants excluded) on the abundance or species richness of three arthropods guilds in the ant-plant *Hirtella myrmecophila*. Significant values are in bold.

Variable	Effect	MS	$F_{1,30}$	P
Abundance of 'tourists'	Plant size	133.8	11.13	**0.002**
	Ants	28.4	2.36	0.135
	Plant size × Ants	12.6	1.05	0.314
	Error	12.0		
Richness of 'tourists'	Plant size	69.2	12.20	**0.002**
	Ants	13.6	2.39	0.132
	Plant size × Ants	5.0	0.88	0.356
	Error	5.7		
Abundance of herbivores	Plant size	84.0	2.36	0.135
	Ants	82.3	2.31	0.139
	Plant size × Ants	257.5	7.23	**0.012**
	Error	35.5		
Richness of herbivores	Plant size	94.1	7.10	**0.012**
	Ants	8.42	0.63	0.432
	Plant size × Ants	80.7	6.08	**0.020**
	Error	13.3		
Abundance of spiders*	Plant size	6.6	0.81	0.375
	Ants	11.5	1.41	0.244
	Plant size × Ants	48.6	5.94	**0.021**
	Error	8.2		

*Excluding *Dipoena* sp. nov.

of spiders was independent of plant size ($R^2 = 0.071$, $F_{1,13} = 0.98$, $P = 0.339$).

Discussion

Effects of mutualistic ants

These results indicate that *A. octoarticulatus* strongly affects the structure of the arthropod community associated with *H. myrmecophila*. As expected, based on previous and similar experiments (e.g. Janzen, 1966; Vasconcelos, 1991; Fonseca, 1994), ant removal resulted in increased abundance of herbivores. However, as far as it can be ascertained, this is first study to show that ants also reduce the abundance of spiders on their host plants. This effect, although previously unnoticed in ant-plants, is probably common, as it is known to occur in non-myrmecophytes as well (Halaj *et al.*, 1997; Mody & Linsenmair, 2004).

Despite having strong effects on spiders and herbivores, *A. octoarticulatus* did not have a significant influence on 'tourists'. This may be in part due to the fact that 'tourists' have a shorter residence time in *H. myrmecophila* and therefore are exposed to ant attacks for a shorter period than are spiders or herbivores. In addition, 'tourists' have a greater mobility than the most common spiders found in *H. myrmecophila* (web-building spiders), as well a greater mobility than some herbivores (e.g. caterpillars), and therefore can more easily escape from ant attacks. Furthermore, in the case of herbivores, *A. octoarticulatus* detects and recognises volatile compounds released by its host plant when the plant is damaged, and the emission of these compounds elicit heavy ant recruitment into the damaged areas (Romero & Izzo, 2004). Such recruitment, induced in response to herbivory, is relatively common among specialised plant-ants (e.g. Agrawal & Rutter, 1998; Lapola *et al.*, 2003; Bruna *et al.*, 2004), but its consequences in affecting the structure of arthropod communities in ant-plants (i.e. affecting some guilds but not others) has not been previously realised. Finally, while 'tourists' are found both in young and old leaves, herbivores feed mainly on young leaves, presumably because older leaves are well defended with chemicals (Izzo & Vasconcelos, 2002). Young *H. myrmecophila* leaves not only have a much greater density of patrolling ants (Izzo & Vasconcelos, 2002), but possibly also a greater concentration of volatile compounds that elicit ant recruitment (Romero & Izzo, 2004).

Plant size influence

Plant size was the only factor affecting the abundance and species richness of 'tourists' in *H. myrmecophila*. Plant size also affected the abundance and species richness of herbivores, but only in plants whose ants were removed. This suggests that, in the absence of ant predation, herbivore populations in *H. myrmecophila* are regulated by plant resources. Similarly, in the absence of ants, the abundance of spiders (excluding *Dipoena* sp. nov.) increased with plant size. In some non-myrmecophytes, spider abundance is affected by plant architecture (Scheidler, 1990), and the
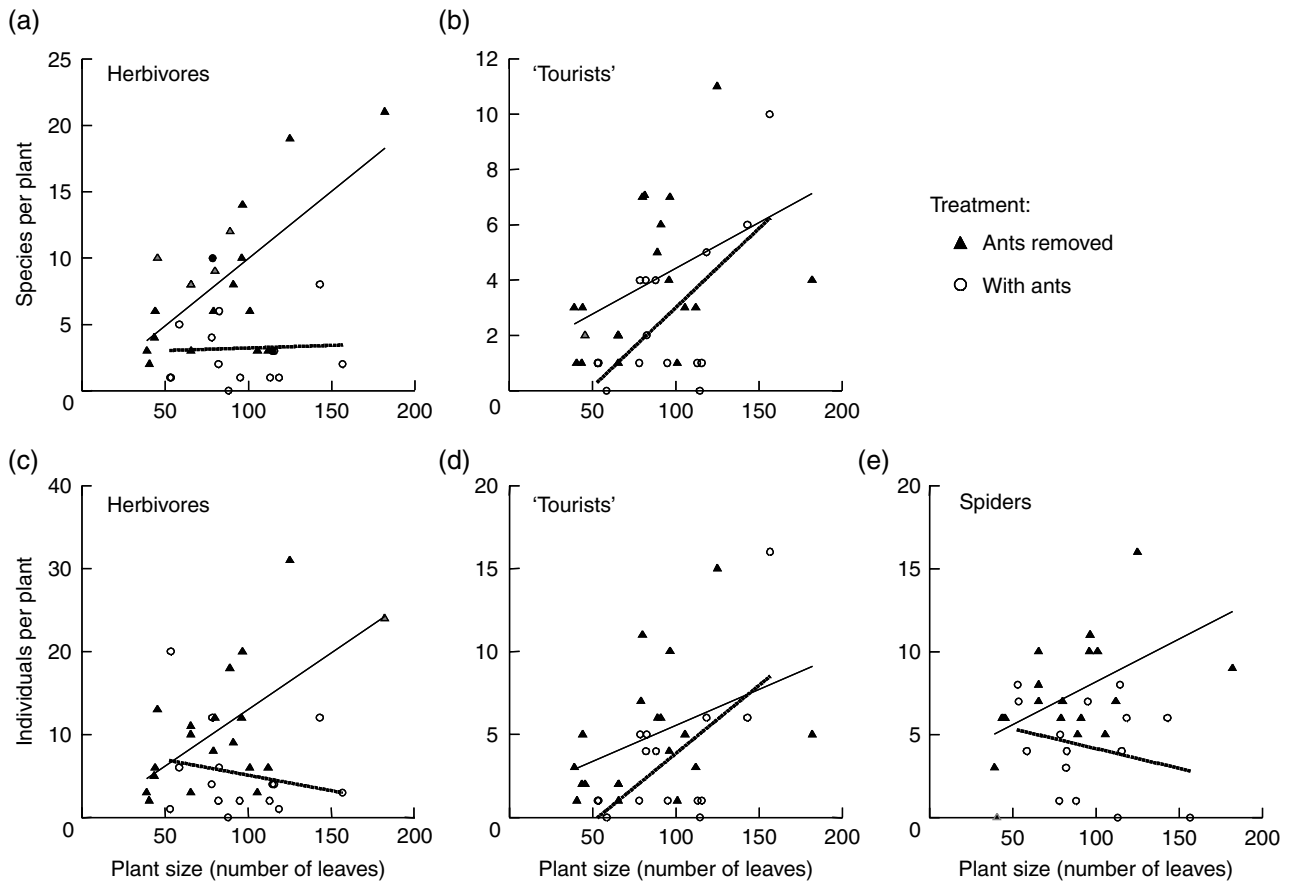
Fig. 1. Relationship between plant size and arthropod abundance and species richness for three different arthropod groups found in *H. myrmecophila*. The lines indicate the tendencies in ant-excluded (solid lines) and ant-maintained plants (dotted lines). Abundance is expressed as the total number individuals found in each plant during five consecutive censuses over a 7-month period, whereas species richness is the cumulative number of morphospecies.

same may apply to ant-excluded *H. myrmecophila* as larger plants have a more complex architecture (i.e. more leaves and branches) than smaller ones. Alternatively, spider abundance in these plants may be regulated by prey abundance, as demonstrated for spiders living on Douglas fir canopies (Halaj *et al.*, 2000). As the most abundant arthropods found in *H. myrmecophila* are herbivores, and as these increased in abundance with plant size in ant-excluded plants (Fig. 1), it is possible that the effect of plant size on spider abundance is in fact an indirect effect (e.g. Gunnarsson, 1996; Halaj *et al.*, 2000), mediated by the effect of plant size on prey abundance.

Contrasting with the situation seen in ant-removed plants, the abundance of herbivores in plants with *Allomerus* remained relatively constant across plant sizes. This finding is somewhat surprising since the smaller plants had similar per-plant herbivore abundances to the larger plants, indicating that the magnitude of ant effects on herbivores increases as plants grow. This may be related to the fact that larger plants house larger ant colonies (Fonseca, 1993, 1999), which, in at least some species, are more efficient in finding and expelling herbivores from the

plant's foliage (Rocha & Bergallo, 1992). Alternatively, or in addition, larger *A. octoarticulatus* colonies may have a proportionally greater demand for food resources and therefore exert a greater pressure on herbivores, as their diet relies heavily on arthropods that venture onto the host-plant foliage (Izzo & Vasconcelos, 2002). In fact, in ants, larger mature colonies often have a greater energetic and nutritional demand than younger colonies, as the production of reproductive alates is costly (Lewis, 1975; Oster & Wilson, 1978).

Similarly, in the presence of ants, the effect (direct or indirect) of plant size on spider abundance disappeared, with similar number of spiders being found in smaller and larger plants (Fig. 1). As with herbivores, this finding is surprising, and reinforces the idea that in *H. myrmecophila* the level of ant defences is related to plant ontogeny. It is possible that *A. octoarticulatus* prey upon or show aggressive behaviours against spiders, although there are no direct observations of this. However, it has been observed that *A. octoarticulatus* constructs foraging tunnels along the stems of its host plant (except on the oldest branches of the plant, which usually

have only older leaves and no ants). Therefore, the constant presence of ants on *H. myrmecophila* stems may in itself inhibit the establishment of spiders, particularly web-building spiders. In addition, ants and spiders may be competing for the same prey (Halaj *et al.*, 1997), and this may render the permanence of spiders on ant-colonised plants even more difficult.

The fourth trophic level

While *A. octoarticulatus* has a negative effect on most spider species, it may also favour those species that specialise on ant predation. In this case, strong evidence was found that *Dipoena* sp. nov. is a specialist predator of *A. octoarticulatus*, and therefore belongs to the fourth trophic level in the *H. myrmecophila*–*A. octoarticulatus* system. This species was almost exclusively found on ant-colonised plants, where the number of spiders increased significantly with plant size, a pattern that contrasts sharply to the one found for the remaining spiders. Studies with *Dipoena banksii*, a specialist predator of the plant-ant *Pheidole bicornis* in *Piper cenoclatun* (Letourneau & Dyer, 1998), indicate that the effect of spider predation on resident ants does not cascade down through the lower trophic levels, but it is not clear if the same applies in the case of the closely related *Dipoena* sp. nov. observed here. *Pheidole bicornis* seems to avoid those leaves colonised by *Dipoena banskii* (Gastreich, 1999), while *A. octoarticulatus*, in contrast, does not display the same behaviour, as all leaves with *Dipoena* sp. nov. were full of ants.

Conclusions

The ant-removal experiment clearly demonstrates that *A. octoarticulatus* reduces the abundance of all arthropods found in its host plant, except those that feed on the ants themselves (i.e. *Dipoena* spiders), or those presenting a very occasional and temporary association with the plant (i.e. 'tourists'). That the effect of ant predation is 'guild dependent' is probably more due to the way different arthropods types use the plant rather than the ability of ants to discriminate between them. *Allomerus octoarticulatus*, like many other plant-ants, is aggressive towards any insect that ventures onto its host plant's foliage, including here species that obviously do not represent a threat to the plant, such as termites and *Drosophila* flies placed experimentally on *H. myrmecophila* leaves (T. J. Izzo, unpublished data). However, the fact that ant activity is mostly concentrated on the younger foliage and branches of *H. myrmecophila* (Izzo & Vasconcelos, 2002) creates 'enemy-free' spaces within the plant. Thus, while ant predation is of great concern for those species depending strongly on young leaves, it is not for the remaining species.

Plant size appears to be only of secondary importance in influencing arthropod community composition in *H. myrmecophila*, as in the presence of ants the observed effects of plant size on herbivores and spiders disappeared. These results strongly suggest that in *H. myrmecophila* there probably exists an ontogenetic change in the level of defence by ants, and further studies are needed to elucidate whether this has implications for plant population dynamics. Finally, the existence of a spider that is specialised to prey upon the major ant associate of *H. myrmecophila* is reported for the first time.

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