

Spiders, Ants and an Amazonian Myrmecophyte: a Tale of Trophic Cascades

by

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ABSTRACT

Plants providing structures in which ants can shelter are often used in studies of trophic cascades. In such systems, predation on ants by specialist top predators may reduce the impact of ants on herbivores, to the plants' detriment. These cascading top predator effects on herbivores and plants may be as follows: (1) numerical, through a reduction in the number of ants upon which the top predator can feed; or (2) functional, through a top predator's effect on the behavioral, morphological, or physiological traits of its ant prey. Detecting the existence of cascading effects in such systems and disentangling these two potential components can be difficult. In this paper, we aim to quantify these components in an Amazonian myrmecophytic system, emphasizing the experimental and analytical procedures that can be used to separate the two components. We describe a trophic cascade from spiders through ants to herbivores using a full factorial experimental design combined with an analysis of the statistical interactions in a two-way analysis of deviance. In addition, we disentangle the density- and trait-mediated interactions using a one-way analysis of deviance on the presence of spiders in relation to (1) the number of ants in domatia and (2) the efficiency of ants in detecting intruders. The experimental and analytical procedures described support the conclusion that the trophic cascades in this system are primarily due to trait- rather than density-mediated indirect interactions.

Keywords: Mutualism, antipredator prey behavior, statistical interactions, food web, cascading effect

INTRODUCTION

Interactions between plants and predators are commonly reported in tropical biomes, such as when plants provide sheltering structures ('domatia') for

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predators. In turn, the predators confer benefits on the plant, generally by preying upon harmful herbivores (McKey 1984, Matos *et al.* 2004, Izzo & Vasconcelos 2005, Grangier *et al.* 2008). When the predators are ants, the plants are called *myrmecophytes* (Janzen 1966), and the benefits include protection against herbivores (Vasconcelos 1991, Fonseca 1994) and competing plants (Suarez *et al.* 1998, Frederickson *et al.* 2005) and the availability of extra nutrients from detritus accumulated by the ants inside the domatia (Janzen 1966, Beattie 1989, Treseder *et al.* 1995). In some cases, these ants do not prey upon the herbivores but, instead, toss them off the plant (Janzen 1966). Exploitative interactions have also been reported between myrmecophytes and their guest ants (Yu & Pierce 1998, Heil & McKey 2003, Palmer & Brody 2007).

These systems frequently include a fourth trophic level, which has not yet been sufficiently studied. In addition to predatory ants and their herbivore prey, top predators, such as spiders and beetles, may also be associated with myrmecophytes (Letourneau & Dyer 1998). Their predation on the intermediate predators (ants) may provoke a cascade that favors the herbivores, hence damaging the plant. Such an indirect effect is termed a 'density-mediated indirect interaction' (DMII), when the effect occurs through a top predator altering the population numbers of its prey (Abrams *et al.* 1996). Conversely, a 'trait-mediated indirect interaction' (TMII) occurs when the influence of a top predator affects the behavioral, morphological, or physiological traits of its prey (Schmitz *et al.* 2004, Griffin & Thaler 2006).

An example of such a four-leveled trophic system is that of the Amazonian myrmecophyte *Hirtella myrmecophila* (Chrysobalanaceae), its herbivores, its exclusive guest ant *Allomerus octoarticulatus* (Myrmicinae), and a specialized ant predator, the spider *Dipoena bryantae* (Theridiidae) (Izzo & Vasconcelos 2005). Indirect interactions in myrmecophyte systems are frequently reported in the literature and classified as either DMII or TMII. Two major issues frequently arise: (1) how to statistically distinguish between direct and indirect interactions; and (2) how to isolate and quantify DMII and TMII. The first issue can be solved using the correct application of statistical procedures; Fig. 1 presents a summary of these techniques using hypothetical data. The second point, teasing apart density and trait effects, requires suitable tests

(Schmitz *et al.* 2004), such as the one described by Peacor & Werner (2001), who measured prey survival as a consequence of risk alone and predation alone in experimental manipulations in the laboratory.

Although experiments allow the independent measurement of trait and density effects, this is not always straightforward in field studies. In the field, uncontrollable external variables make unbiased data collection difficult and mask cause and effect. However, field experiments are appealing because they come so close to biological reality. An ideal approach would be to use observational experiments coupled with statistical procedures to independently account for trait and density effects. As Ruxton & Colegrave (2006) observe, observational (mensurative) experiments are an obvious choice when “[...]”

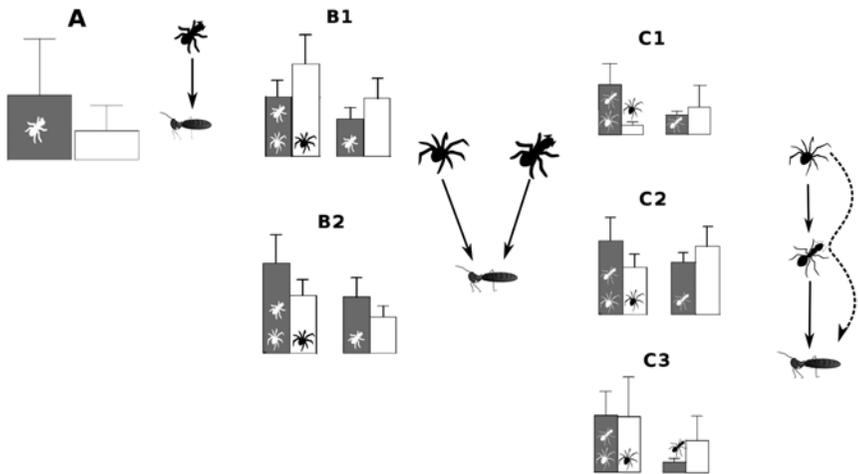


Fig. 1: Statistical outcomes allowing the detection of trophic cascades in a food web. In the hypothetical graphs, the y-axis measures the lower trophic level (*i.e.*, herbivory) and the x-axis (bars) represents the presence/absence of the upper trophic level(s). (A) Direct interactions (continuous arrows) can be spotted by a one-way analysis of variance (or deviance) between any two levels of a food web, *e.g.*, the consumer on the x-axis and its prey (or plant) on the y-axis. (B & C) When two consumers are involved, a two-way analysis of variance can be used; each consumer being a factor on the x-axis and the prey (or plant) involved on the y-axis. In such cases there are two possible outcomes: (direct interaction, B) no statistical interaction between factors (consumers) on the x-axis produces pairs of bars presenting a similar pattern, *i.e.*, grey bars are always smaller than white bars (B1) or vice versa (B2); and indirect interaction (dashed arrow), C) significant statistical interaction between factors (consumers) on the x-axis produce pairs of bars presenting different patterns, *i.e.*, the grey bar is larger than the white bar on one side and smaller on the other (C1) or vice versa (C2), or even the grey bar and the white bar are equivalent on one side and different on the other (C3).

we are dealing with organisms that are likely to be stressed or damaged by handling [...]". Observational techniques avoid the risk of unintended effects arising from handling animals in laboratory experiments. In this study, our goal was to quantify the DMIs and TMIs in an observational field experiment on the myrmecophytic system described above, with an emphasis on the experimental and analytical procedures employed.

In the field, we evaluated the evidence for indirect interactions by measuring the effects of the top predators (spiders) on the efficiency of the intermediate predators (ants) in lessening the impacts of herbivores on their host-plant leaves. Subsequently, we disentangled these indirect interactions into DMIs and TMIs. We evaluated the DMIs by measuring the effect of spiders on the abundance of ants living inside the domatia of plants. The TMIs were evaluated by measuring the effect of the top predator on the time these ants took to locate intruders on the plant leaf.

MATERIAL AND METHODS

Study site

The experiment was performed as part of the Biological Dynamics of Forest Fragments Project (Bierregaard *et al.* 2001) at a site 80 km north of Manaus, Central Amazonia, Brazil (2°24'S, 59°43'W), in a 10,000 ha region of continuous, undisturbed Amazonian upland rain forest, which was designated exclusively for scientific research in 1984. The area consists of typical tropical moist forest and has a 35 to 40 m tall canopy, with emergent trees as high as 50 m (Laurance 2001) and an open understory characterized by the abundance of stemless palms. It is a lowland (50-100 m elevation), gently sloping with many streamlets and generally poor latosol soils. The annual rainfall is 1900-2300 mm, with a dry season between July and September and slightly fluctuating mean daily temperatures between 26-28°C. Bierregaard *et al.* (2001) provide details of this site under the code '1501' or camp Km 41.

The biological system

The ecosystem studied included the Amazonian myrmecophyte *H. myrmecophila* (Chrysobalanaceae), a small (<10 m) understory tree commonly found in non-flooded forests of the central Amazon. Its leaves have leaf-pouches

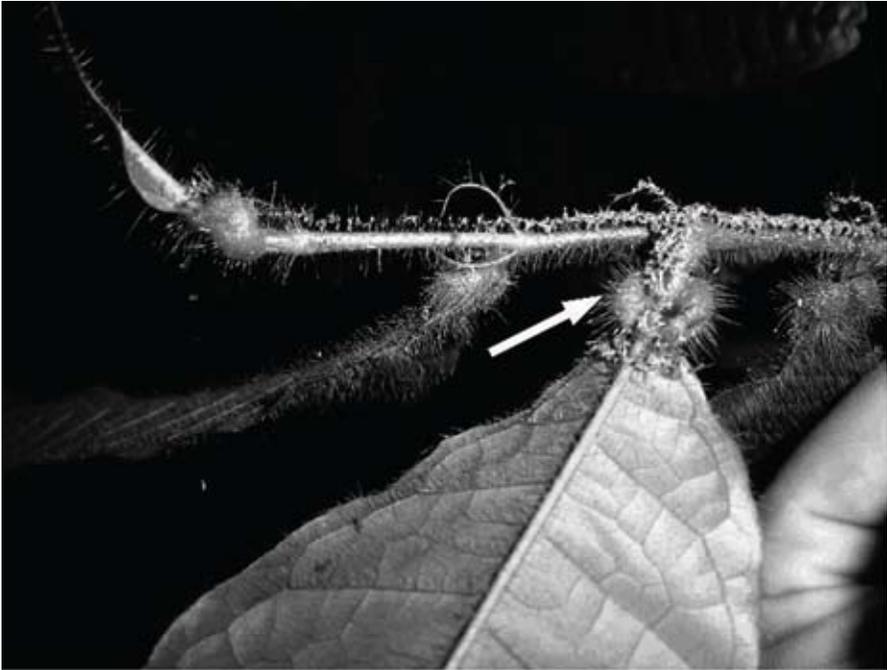


Fig. 2: Leaves of *Hirtella myrmecophila* with domatia, as indicated by the white arrow.

(domatia; Fig. 2), with the leaf blade rolled to form two tubular chambers (Fonseca 1999). In old leaves, the domatium dries and falls off (Romero & Izzo 2004). In Km 41, this plant is almost exclusively associated with the ant *A. octoarticulatus* (Fonseca 1999, Izzo & Vasconcelos 2002), a Myrmicinae predatory ant that only nests in myrmecophytes. *H. myrmecophila* does not produce any food for the ant, and *A. octoarticulatus* feeds mainly on insects that venture onto the leaves (Izzo & Vasconcelos 2002), never foraging away from the host plant. On the leaves, the ants prey upon herbivores, thereby protecting the host plant against herbivorous attack (Izzo & Vasconcelos 2002). Many species of web-building spiders commonly establish their webs on myrmecophytes (Fowler & Venticinque 1996). The web-building spider *D. bryantae* (Theridiidae) often builds a web near the domatium entrance and attracts its ant prey by vibrating the leaf surface. When an ant leaves the domatium, it is attacked and immediately wrapped in silk for later consumption (Izzo & Vasconcelos 2005). Several spiders may inhabit a single plant and feed on ants in this way (Izzo & Vasconcelos 2005).

The experiment

We studied the myrmecophyte-invertebrate association described above, in which spiders are the top predators and ants are the intermediate predators. On selected leaves, we examined the behavior of foraging ants toward intruders (following Oliveira *et al.* 1987 and Izzo & Vasconcelos 2002) using live workers of the termite *Nasutitermes* sp. as bait (Dejean *et al.* 2001a,b, Cogni *et al.* 2003). According to Dejean *et al.* (2001a), in a system similar to that described above (*Allomerus-Hirtella*), ants patrol the entire plant containing their colony and are able to detect a feeding termite. Moreover, termites can be used as bait (Dejean *et al.* 2001a,b) because the ants, *A. octoarticulatus*, are able to detect and feed on any insect that ventures onto the leaves (Izzo & Vasconcelos 2002).

In order to measure any indirect interactions, we set up a full factorial observational experiment in which treatments were used as found naturally in the study system to test whether spiders and ants would interact in a way that affects the amount of herbivory suffered by the myrmecophyte leaf. Pairs of leaves from different individual plants were chosen to represent the four possible combinations of spider present or absent \times ants present or absent. This experimental design is rare in studies analyzing myrmecophytes and their invertebrate partners. It was chosen here in order to explicitly test the combined effects of spider-ant interactions on herbivory (Fig. 1).

After evaluating the evidence for indirect interactions, it is necessary to distinguish between density- and trait-mediated indirect interactions (DMIIs and TMIIIs, respectively). To test for DMIIs, we looked to see if the presence of a spider on a leaf affected the number of ants inhabiting the domatia on that leaf. To test for TMIIIs, we examined whether the presence of a spider on a leaf affected the speed with which intruders (*i.e.*, termite baits) were located by ants inhabiting that leaf. A termite was considered 'located' if it was touched by an ant that was patrolling the leaf.

We sampled 22 individual plants of *H. myrmecophila* (0.5-2.5 m tall). On each plant, we selected a single pair of opposing, domatia-bearing leaves, with one leaf of each experimental pair having a resident spider (*D. bryantae*), and the other leaf having no resident spider. Each pair of leaves represented a single ant colony. Leaves showed varying degrees of herbivory, either in the form of

missing, bitten portions or necrotized areas. A single *Nasutitermes* sp. termite worker (third instar and beyond) was placed on the upper surface of each leaf. We recorded the time elapsed from placement of the termite intruder until it was first touched by any *A. octoarticulatus* ant patrolling the leaf. Each leaf was observed for a maximum of 300 seconds.

At the end of the observation period, the experimental leaves were taken to the laboratory, where the number of ants inside the domatia were counted, and the percentage of foliar area showing clear physical injuries, typical of an attack by herbivores, was measured. Foliar area was measured by analyzing digital photographs of the leaves with *ImageTool* (University of Texas Health Science Center, San Antonio, Texas, <http://ddsdx.uthscsa.edu/dig/itdesc.html>).

Statistical analyses: Verifying the existence of indirect interactions

Indirect interactions would be suggested if herbivory on leaves was affected by both ants and spiders, with the effects of ants depending on the presence of a spider. That is, herbivory observed in the presence of ants should be greater when a spider was present than when it was absent. In statistical terms, there would be a significant interaction between the x-variables, *presence of a spider* and *presence of ants*, affecting the y-variable, *percentage of herbivory*.

In order to explicitly test this, we built a statistical model including the x-variables referred to above and their first order interaction and used Generalized Linear Modeling with binomial errors, corrected for overdispersion and a quasibinomial distribution. Plant individuals were included in the model as a blocking factor, as an acknowledgement that many other unmeasured factors could affect the system under study; these could vary between individual plants.

Subsequent residual analyses confirmed the suitability of the models and the choice of error distribution, following the rationale of Crawley (2007). Model simplification was achieved by extracting non-significant terms ($P > 0.05$) from the model, starting with the term explaining the least deviance. Each term deletion was followed by an Analysis of Deviance with χ^2 test, in order to recalculate the deviance explained by the remaining terms. In order to prevent misinterpretation arising from redundancy of terms, distinct models

were built and tested, with each model including all explanatory variables, but differing from the others by the order in which the variables were included in the model. A non-significant simple term was retained in the model if it belonged to a significant interaction term. Analyses were performed using R Development Core Team (2008).

Statistical analyses: Disentangling DMIs and TMIs

After confirming that the presence of spiders affected the ability of ants to limit herbivory, we sought to determine whether this effect was due to the effect of spiders on the number of ants inhabiting the domatia (*i.e.*, DMIs), the ability of the ants to detect the presence of intruders (*i.e.*, TMIs), or both. This was performed by analyzing the data using Generalized Linear Models as described above, using an appropriate error distribution.

The presence of DMIs was tested using a model where the number of ants in the domatia was entered as the y-variable and the presence of a spider as the x-variable. Individual plants were entered as a blocking factor. Due to the nature of the y-variable data, modeling was performed using Poisson errors and a log link, subsequently corrected for overdispersion using a quasi-Poisson distribution.

The presence of TMIs was evaluated by examining the effect of the presence/absence of a spider on the time (in seconds) taken by ants to locate and touch a termite intruder after it was placed on the leaf. This reveals the effect of spiders on the promptness of intruder location by ants and, hence, how spiders indirectly affect potential herbivory threats.

For this analysis, data were subjected to survival analysis with a Weibull distribution (Crawley 2007), performed using the survival package in R Development Core Team (2008). Survival analysis, or failure time data analysis, involves the statistical analysis of the time from a well-defined time origin to the occurrence of some given event or end-point (Martinussen & Sheike 2006). In this case, the time origin was the moment when a termite was placed on a leaf, and the end-point was the moment when an ant first touched the termite. This analysis examined whether the presence of a spider affected the efficiency of ants patrolling the plant leaves. We were therefore examining the “survival” of a termite on the leaf, with its “death” being considered to happen at the moment it was first touched by an ant. A positive result would

Table 1: Effect of ants, spiders and the interaction between them on the percent of foliar area presumably injured by herbivores on *H. myrmecophila*. Analysis of deviance of the minimal adequate model (MAM) using generalized linear modeling and quasibinomial error distribution.

Source of variation	d.f.	X^2	P -values
MAM	24	7.20	6.65 ³³
Plant (Block)	21	5.11	1.50 ²⁴
ants	1	0.89	6.50 ⁰⁸
spider	1	0.51	4.42 ⁰⁵
ants*spider	1	0.13	0.033
Error	19		
Total	44		

Table 2: Effect of spiders on the time taken by ants to locate and touch a termite intruder after it was placed on leaves of *Hirtella myrmecophila*. Data were subjected to survival analysis with a Weibull distribution.

Source of variation	d.f.	X^2	P -values
Model	22	144.54	1.02 ¹²
Plant (Block)	21	104.52	4.54 ¹²
spider	1	10.08	0.0015
Error	22		
Total	44		

indicate that the corresponding regulatory force (TMIs) was acting on this system to change the behavior of the ants. Similar uses of this analysis in a biological context can be found in Miramontes & DeSouza (1996), DeSouza *et al.* (2001) and DeSouza *et al.* (2009).

RESULTS

A total of 44 leaves (22 plants) of *H. myrmecophila* were used in the experiment. All leaves had a single domatium at their base, which was frequently used as a nesting site by *A. octoarticulatus* ants. *D. bryantae* spiders were present on 22 of these leaves, with each leaf holding only a single spider. Spiders were normally found hanging from a silk thread directly in front of the opening of the domatium. The number of ants per domatium ranged from zero to 111, with a mean of 18.9. Among the 44 leaves studied, 19 were inhabited by spiders and ants, three had spiders but no ants, 17 had ants but no spiders, and five had no ants and no spiders.

The presence of ants and spiders affected herbivory on leaves of *H. myrmecophila*. Ants and spiders produced significant ($P=0.033$; Table 1) interdepen-

dent effects on the y-variable (herbivory). This interdependence can be clearly seen in Fig. 3: in the absence of a spider, the presence of ants substantially reduced herbivory, but this effect was not observed when a spider was present. In addition, part of the deviance in herbivory was explained by the blocking factor *plant* (Table 1), meaning that factors associated with the plant itself (other than the numbers of ants and spiders) also affected herbivores. This confirms our prediction above that the factors under study (*presence of ants* or *spiders*) could account for significant portions of the deviance in herbivory even when this significance was reduced by the influence of the blocking factor *plant*. That is, spiders and ants played an important role in herbivory on these plants, whatever the importance of other factors not measured is.

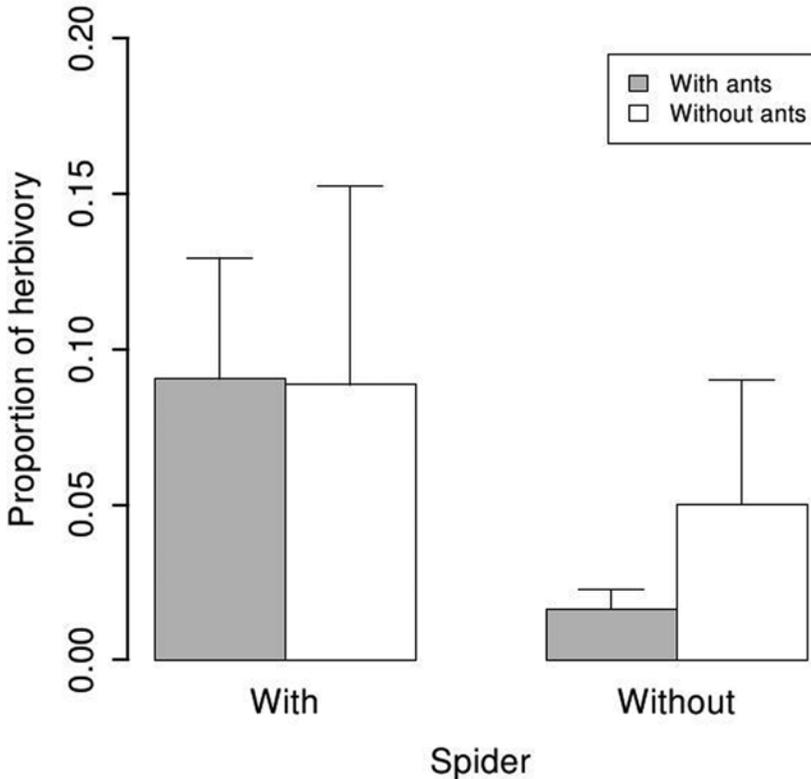


Fig. 3: Proportion of leaf area consumed in leaves of *Hirtella myrmecophila* as a function of the presence/absence of a spider and ants. Interaction between factors is statistically significant; see Table 1.

The number of ants inhabiting the domatia was not affected by the presence of a spider ($P = 0.31$, $\chi^2 = 10.86$). However, the presence of a spider increased the time taken for ants to locate and touch a termite intruder (Table 2).

There is, therefore, an indirect effect of spider presence on the impact of herbivores (Fig. 3). This indirect effect was due to spiders causing an increase in the time taken by ants to locate intruders on the experimental leaves (Table 2) rather than their affecting the number of ants in the domatia.

DISCUSSION

Herbivory on leaves was affected by both ants and spiders, with the effects of ants depending significantly on the presence or absence of the spiders (Table 1). Interestingly, this significant interaction was important in confirming indirect effects. If no significant interaction had been detected, pairs of bars in Fig. 3 would have shown the same pattern (e.g., grey bars smaller than white bars, or vice versa) either in the presence or absence of a spider, as depicted in Fig. 1B. This would indicate that the effects of the ants on herbivory were independent of the effect of the spiders and, hence, that spiders were directly affecting herbivory. Full factorial experiments are, however, required to properly explore the statistical interactions between categories of variables. Therefore, we suggest that future experiments measuring trophic cascades that are similar to the one described here should employ full factorial experiments if categorical variables are under scrutiny (e.g., presence/absence of ants \times presence/absence of spiders).

An indirect effect of spiders on herbivores is evident in Fig. 3. In the absence of spiders, the extent of herbivory on leaves the domatia of which contained ants was less than that on leaves without ants (Fonseca 1994, Grangier *et al.* 2008, Rosumek *et al.* 2009), an effect completely absent when spiders were present. That is, the presence of a spider reduced herbivory. Because the spider itself is not an herbivore but, rather, a predator of the ants (Izzo & Vasconcelos 2005), one can conclude that herbivores may be profiting from the threats that spiders impose upon the ants.

Such threats and their consequences provide the likely mechanisms responsible for the trophic cascade reported here as follows: (1) spiders can reduce the number of the ants and, consequently, their impact on herbivores; and (2) ants, recognizing the presence of a spider, would be less likely to leave the

domatia, reducing the frequency of their attacks on herbivores. These effects correspond to DMIs and TMIs, respectively.

Our next question, therefore, is whether this trophic cascade was the result of one or both mechanisms. A closer look at our results seems to favor a single mechanism explanation: that the presence of a spider hinders the location of the intruders by the ants. Because the number of ants was not affected by the presence of a spider ($P = 0.31$), the indirect effects of spiders on herbivores (Fig. 3) are not due to the number of ants on a leaf. It seems reasonable to conclude that the number of ants did not influence these indirect interactions and that DMIs did not seem to operate.

Conversely, because the presence of a spider delayed the location of the intruder by the ants (Table 2), this suggests that TMIs played a crucial role in determining the indirect interaction observed in Figure 3. Alternatively, TMIs would apply if spiders chose leaves with less aggressive ants, perhaps to avoid being stung by *A. octoarticulatus*. However, *D. bryantae* is a sit-and-wait predator and usually hunts very active prey, as do other sit-and-wait spiders (Schmitz & Suttle 2001). Therefore, the hypothesis that the absence of TMIs is because of less aggressive ants is unsupported.

Similar results, favoring TMIs over DMIs, were also found by Gastreich (1999) and Letourneau & Dyer (1998), working on *Piper* sp. plants and their associated spiders, ants, and herbivores in Costa Rica. At first glance, the absence of measurable density effects of a predator upon its prey seems odd. However, a single colony of *A. octoarticulatus* ants occupies more than one domatia in the same plant; normally, one colony occupies all domatia of a given plant (Fonseca 1999, Izzo & Vasconcelos 2002). Ants lost to predation, therefore, may be quickly replaced by nestmates from other domatia, damping the spider effect on ant density in a single leaf. In fact, Dejean *et al.* (2001a) observed that *Allomerus decemarticulatus* patrol all the leaves of the *Hirtella physophora*. Moreover, as proposed by Fonseca (1999), colony size of *A. octoarticulatus* seems to be controlled primarily by the number of domatia. In addition, if the predation rate for *D. bryantae* spiders upon *A. octoarticulatus* ants is as low as that showed by *D. banksii* spiders (one ant every three days, Letourneau & Dyer 1998), DMIs should not be easily detected in such a system, whereas the importance of the TMIs would be clear.

The assessment of the relative importance of distinct indirect effects, however, must be treated with caution. As Werner & Peacor (2003) warn, although it is essential to understand the underlying nature of trophic cascades, this focus can be counterproductive. What is needed ‘to understand how density and trait effects interact so that this interaction can be incorporated in dynamic models’, is to dichotomize these effects (Werner & Peacor 2003). This is precisely our approach here. We present a simple and effective way to disentangle TMIs and DMIs and hope that our reasoning will shed some light on the following: (1) studies on Amazonian myrmecophytes and their associated fauna; and (2) methods to assess the relative importance of indirect effects in trophic cascades. In conclusion, the experimental and analytical procedures described here show that the trophic cascades in this system are due primarily to trait- rather than density-mediated indirect interactions.

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