



Cascading trait-mediation: disruption of a trait-mediated mutualism by parasite-induced behavioral modification

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Trait-mediated indirect interactions (TMII) are important driving-forces causing trophic cascades in aquatic and terrestrial food webs. Furthermore, since most biological communities are not simple food chains but complex networks of interactions, one TMII within a community might easily be influenced by another TMII. In other words, TMII themselves can be cascades with potential implications for community dynamics. Here we report on one of such cascade, where a parasitic fly induces behavioral changes that disrupt a trait-mediated ant–hemipteran mutualism. We show that during parasite-induced low-activity periods, the ant *Azteca instabilis* fails to protect its mutualistic scale-insect partner against predatory ladybeetles. Thus, in the presence of the parasite, ladybeetles ate as many scales in ant-patrolled plants as they did in ant-free plants. These results demonstrate how, through a cascade of trait-mediated interactions, associations between members of a community can be drastically altered.

Cascading effects in food webs are common and well-documented. In tritrophic systems, for example, predators or parasites can have cascading positive effects on a plant population by reducing herbivore pressure (Shurin et al. 2002). These trophic cascades can be triggered either by an actual reduction in herbivore densities, i.e. a density-mediated indirect interaction (DMII) (Abrams 1995, Werner and Peacor 2003) or by changes in herbivore behavioral traits induced by the presence of predators or parasites, i.e. a trait-mediated indirect interaction (TMII) (Abrams 1995, Peacor and Werner 2001, Werner and Peacor 2003, Schmitz et al. 2004). The behavior and consequences of both types of trophic cascades have been broadly studied in terrestrial and aquatic communities (Brett and Goldman 1996, Shurin et al. 2002, Schmitz et al. 2004).

However, most biological communities are not simple tritrophic chains but complex networks of interactions (Polis 1991). Accordingly, multi-trophic communities with multiple and interacting density-mediated effects have been extensively studied (Schoener 1989, Power 1990, Letourneau and Dyer 1998). What is needed next is a more thorough understanding of the consequences of increasing the number of species or links that create new trait-mediated effects or through which trait-mediated effects propagate (Abrams 1993, 1995, LeBrun and Feener 2002). Theoretical studies have modeled four species food webs containing two or more trait-mediated links for some time (Abrams 1992, Abrams and Matsuda 1993). However, there still remains a dearth of empirical studies tracing how the effects of two or more TMII interact and propagate through ecological communities.

Interesting dynamics, like the positive feedbacks found in ant community assemblages (LeBrun and Feener 2002), might arise when multiple non-consumptive effects interact within a community. For example, if through attempting to escape the attack of a predator the herbivore reduces its feeding rate, there would be a positive TMII between the predator and the plant. However, if a top predator is introduced into the system and its presence causes the first predator to reduce its feeding rate, the first TMII would be disrupted, the herbivore could resume its feeding activities, and the plant would again suffer higher levels of herbivory. In such a situation, the top predator has introduced a new trait-mediated effect that interacts with another trait-mediated effect. Such an interaction of two TMII that has cascading community-wide effects is what we are calling here cascading trait-mediation.

What would be the effect of adding species that create new TMII to competitive and mutualistic associations that are already trait-mediated? For example, behavioral changes induced by predation risk might alter the ability of a superior competitor to acquire resources, allowing the inferior competitor to flourish in the presence of a predator (Feener 1981, Werner 1991, Peacor and Werner 1997, Werner and Peacor 2003). Furthermore, many mutualisms, like ant–hemipteran and ant–plant mutualisms, are also trait-mediated. While ants receive a direct benefit, in the form of honeydew or extra-floral nectar, the benefit received by their mutualistic partners is indirect and trait-mediated. In these associations, plants and hemipterans alike gain enemy-free space not because their natural enemies' density is reduced by the ants, but rather because of the behavioral changes

induced by the constant ant patrolling and the resulting difficulty natural enemies have in accessing their food. Adding a top-predator or parasite to such systems could trigger cascading trait-mediations that could potentially reverse back competitive outcomes and disrupt mutualism associations.

Here we examined the community-wide effects of a cascading trait-mediation triggered by the presence of an ant parasitoid on an insect community in a coffee plantation in Chiapas, Mexico. In our study site, the tree-nesting ant, *Azteca instabilis* normally protects the coffee green scale, *Coccus viridis*, by constantly harassing the predatory ladybeetle, *Azya orbiger*a (Coleoptera, Coccinellidae). However, previous studies have shown that the presence of the parasitoid fly *Pseudacteon* sp. (Diptera, Phoridae) drastically reduces ant activity levels (Philpott et al. 2004). Given that phorids are very active around *A. instabilis* nests during the rainy season, when both scale and beetle populations are at its highest, and ant activity is drastically reduced for up to 90 min even after short periods of phorid attacks (Philpott 2005, Philpott et al. 2009), we wanted to determine how this parasite-induced behavioral change altered the interactions between *A. instabilis* and the predatory ladybeetle, *A. orbiger*a. With respect to the cascading trait-mediation, we specifically asked three questions: 1) how does phorid presence affect ant activity? 2) how does the reduction of ant activity influence the interactions between ants and ladybeetles? And 3) does phorid fly presence allow ladybeetles to prey upon ant-tended scales? We hypothesized that in the presence of phorid flies, ants would fail to protect their scale insect partners against predation by the ladybird beetle. The final consequence of this cascading trait-mediated effect would be that the mutualism between *C. viridis* and *A. instabilis* would be disrupted and *A. orbiger*a would gain access to otherwise non-accessible prey (Fig. 1).

Methods

Study site

Experiments were conducted in a 300 ha organic shaded coffee farm located in southwestern Chiapas, Mexico

(15°11'N, 92°20'W). The site is 900–1150 m in elevation and receives ~4500 mm of rainfall annually. Experiments took place during the rainy season between June and August 2008.

For all laboratory experiments, small pieces of *A. instabilis* colonies were collected from the field and broken into roughly 10 cm in diameter fragments (details in Lierre and Perfecto 2008). Fragments of this size contain a large number of workers, larvae, and pupae, and function as artificial nests that maintain regular activities of food collection and nest defense, and are self-sustainable for several weeks. Fragments were placed in plastic containers with sides treated with Insect-a-Slip Insect Barrier and the top edges coated with Tanglefoot.

All *A. orbiger*a adults used were collected from the field and maintained in the laboratory in insect rearing cages. They were fed *C. viridis* scales on fresh leaves daily, to excess. *Pseudacteon* flies were collected in the field near *A. instabilis* nests between 8–11 a.m. and were introduced to the experimental arenas before 1 p.m. on the same day they were collected.

How does phorid presence affect ant activity?

To confirm Philpott et al.'s (2004) results, which show that in the field *A. instabilis* activity is significantly reduced by the presence of phorid flies, we conducted an ant response experiment to determine how the presence of *Pseudacteon* sp. reduced ant activity levels under controlled laboratory conditions. Coffee branches with one or two *C. viridis* infested leaves were collected from the field and 'planted' on a wire base inside a 10 cm tall, 6.5 cm Ø plastic cup. The 'planted' twig was then placed within the larger plastic container holding the artificial *A. instabilis* nest, and together they were placed in the center of transparent 60 × 60 × 60 cm insect rearing cages. Ant activity was recorded as the number of ants crossing a given point on the 'planted' twig in a 1-min period. Ant activity was first evaluated in the absence of phorid flies; two phorid flies were then released inside the cages. Ant activity was reassessed at 0, 5, 10, 15, 20, 30, 60 and 120 min after the phorids were released. There were sixteen replicates for this experiment. To minimize potential confounding light or temperature variation, the replicates were conducted one at a time and were spread out

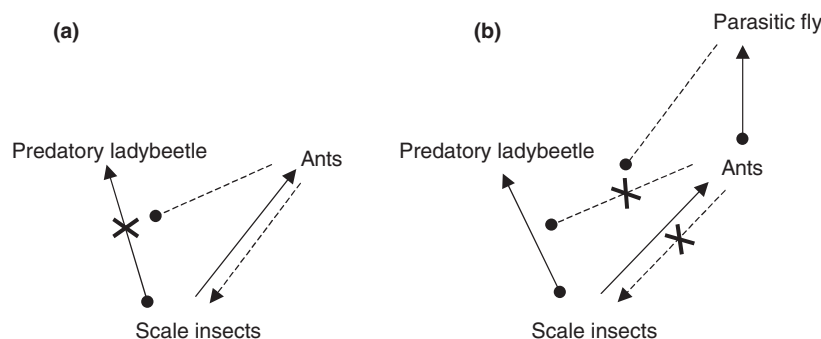


Figure 1. Hypothesized interactions and cascading effect of the parasitic fly (*Pseudacteon* sp.) on the trait-mediated mutualism between *Azteca instabilis* and *Coccus viridis*. (a) The ladybeetle, *Azya orbiger*a, avoids ant-tended scale colonies because of the risk of ant attack. In this way, scale insects gain enemy-free space by behavioral changes in the ladybeetle induced by the presence of the ants: TMII mutualism. (b) If the presence of the parasite reduces ant activity, ladybeetles would be released from ant influence; the mutualism would be disrupted and the ladybeetles would gain access to scales. Solid arrows represent direct interactions, dashed lines represent indirect interactions. Circles represent negative effects and arrows represent positive effects.

throughout six days between 30 June and 12 July 2008. We completed one to three replicates each day, starting around 11 a.m. Ant activity before and during each time period after phorid introduction was compared using a repeated measures mixed linear model, using 'trial' as the subject variable, 'ant activity' as dependent variable, and 'time' (before phorid introduction, 0, 5, 10, 20, 30, 60 and 120 min) and 'day' (1–6) as fixed effects.

How does the parasite-induced reduction of activity influence in the interactions between ants and ladybeetles?

We evaluated the interaction between ants and *A. orbiger* adults in 27 ant-tended scale-infested coffee bushes in the field. To understand phorid fly influences on ant activity and indirect influences on *A. orbiger* behavior, we evaluated ant–coccinellid interactions before and after phorids arrived. First, ant activity in the absence of phorid parasitoids was measured as the number of *A. instabilis* that crossed a single point 'a' (approximately 30–45 cm from the ground) on a coffee branch within a 2-min period. One *A. orbiger* adult was then placed at that point, and the occupation time of the beetle in the coffee plant was noted. Additionally, interactions were qualitatively categorized as either a) ants attacking, capturing and killing the beetle, b) ants attacking the beetle causing it to fall or fly away, or c) beetle flying away on its own. Any beetle that did not leave the bush after 10 min was recorded as occupying the bush for 10 min and leaving on its own.

In order to evaluate the effect of ant parasitoids on the ant–beetle interactions, we then smashed one ant in the plant to attract a phorid fly (Philpott et al. 2004). We observed that the initial *A. instabilis* response to phorid flies includes running to a hiding place or back towards the nest, so we waited four min after the first phorid appeared to measure ant activity (again, number of ants crossing point a during a 2-min period). Then, a new *A. orbiger* adult was placed at point a, and occupation time and interaction type were recorded.

Since the response of ants to their phorid parasitoids is commonly found to be consistent, irrespective of the number of attacking flies (Feener and Brown 1992, Morrison et al. 2000, LeBrun and Feener 2002, Orr et al. 2003) we did not try to control the number of phorids that arrived or take note if multiple flies were present during a trial. If phorids did not appear within the first five min, one additional ant was smashed every five min. If no phorids appeared within 15 min, or if all phorids left before the observation period, the trial was ended.

Beetle occupation time and ant activity were log-transformed to meet the conditions of normality and then a linear regression was used to evaluate the relationship these two variables with and without phorids. However, we observed that somewhere between twelve and eighteen ants/2-min period there appeared to be a discontinuity or threshold in the data, below which ants did not seem to affect the time beetles stayed in the plants. The exact value of this ant-activity 'threshold' was not relevant for our study and therefore we did not attempt to statistically locate it. What was important to our study was the fact that for low ant activity values the interaction between the two variables was different than for high ant activity values. Therefore, in addition

to the regression between the whole data, we performed two separate linear regressions, one above and one below 15 ants/2-min period. Ant–beetle interactions were then compared with χ^2 contingency tables to determine if beetles were as likely to leave a plant on their own as due to ant harassment below and above these ant-activity 'threshold'.

Does phorid fly presence allow ladybeetles to prey upon ant-tended scales?

To establish whether the presence of *Pseudacteon* sp. enabled *A. orbiger* adults to consume ant-tended scales, we performed a laboratory predation experiment. We collected *C. viridis*-infested coffee twigs from the field and counted the number of adult scales; we used only those twigs that had approximately 100 adult scales. The twigs were 'planted' as described above, and then placed inside rearing cages. The twigs were randomly assigned to one of three treatment cages: 1) no ants and no phorids, 2) with ants and no phorids, and 3) with ants and with phorids. There were 14 replicates of each treatment.

Once the ants were actively tending the scales in the rearing cages, one coccinellid adult was randomly assigned and released into each of the three treatment cages. For the treatments with phorids, two flies were released in each cage simultaneously with the coccinellid adult. After 24 h, we counted the remaining adult scales and calculated the number of scales eaten during this period. To detect difference between treatment means we used an ANOVA test and then a Tukey test for post-hoc comparisons.

Results

How does phorid presence affect ant activity?

Time after phorid introduction had a significant effect on ant activity ($F_8 = 9.415$, $p < 0.0001$) and this result did not depend on the day the trial was performed ($F_5 = 0.426$, $p = 0.820$). Ant activity ($16.19 \text{ ants min}^{-1} \pm 2.21 \text{ SE}$) was halved five minutes after the phorids were released into the cages ($8.4 \text{ ants min}^{-1} \pm 1.4 \text{ SE}$) and stayed around that level for the remainder of the observation period (2 h) (Fig 2).

How does the parasite-induced reduction of activity influence the interactions between ants and ladybeetles?

Though we never observed any beetles being caught or killed by ants, there was a strong negative relationship between ant activity and beetle occupation time ($R^2 = 0.72$, $F_{1,26} = 69.2$, $p < 0.00001$). There appears to be a threshold of ant activity below which ants do not seem to affect the time beetles stayed in the plants and this is reflected by the poorer fit to the linear regression at low ant-activity values (Fig. 3). Below fifteen ants per 2-min period, ant activity and beetle occupation time had a very weak and non-significant relationship ($R^2 = 0.0192$, $F_{1,11} = 0.47$, $p = 0.5$) and beetles were as likely to fly on their own as they were due to ant attacks (26 non-attacks vs 15 attacks;

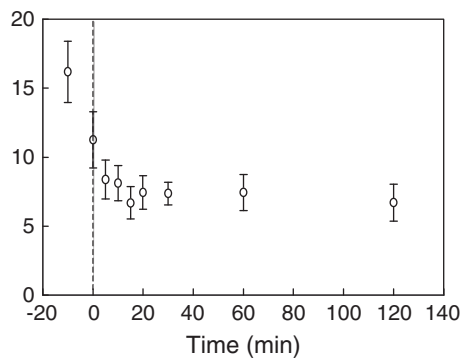


Figure 2. Effect of *Pseudacteon* phorid presence on *Azteca instabilis* activity levels. Data show mean \pm SE ($n = 16$). Experiments were conducted in the lab inside rearing cages. Dashed line indicates when the phorids (two per cage) were released. There was a significant effect of time after phorid introduction on ant activity ($F_8 = 9.415$, $p < 0.0001$).

$\chi^2 p > 0.05$). Contrastingly, above this value of ant activity there was a strong negative relationship between ant activity and beetle occupation time ($R^2 = 0.627$, $F_{1,12} = 20.21$, $p = 0.0007$) (Fig. 3a) and beetles always flew away or fell off of the plant to escape harassment (0 non-attacks vs 21 attacks; $\chi^2 p < 0.001$). After phorids arrived, ant activity was reduced below the threshold in all but two trials; as a result, beetles were no longer affected by ants ($R^2 = 0.091$, $F_{1,23} = 2.32$, $p = 0.141$) (Fig. 3b).

Does phorid fly presence allow ladybeetles to prey upon ant-tended scales?

The number of scales eaten by *A. orbigera* was significantly affected by treatment in the consumption experiment (ANOVA, $F_2 = 6.651$, $p = 0.004$) (Fig. 4). The presence of tending ants significantly reduced the number of scales eaten (post-hoc Tukey-test: $p = 0.005$). However, when phorids were present, the protective effect of *A. instabilis* disappeared and *A. orbigera* was able to prey as many scales as in the treatment without ants (post-hoc Tukey-test, $p = 0.836$).

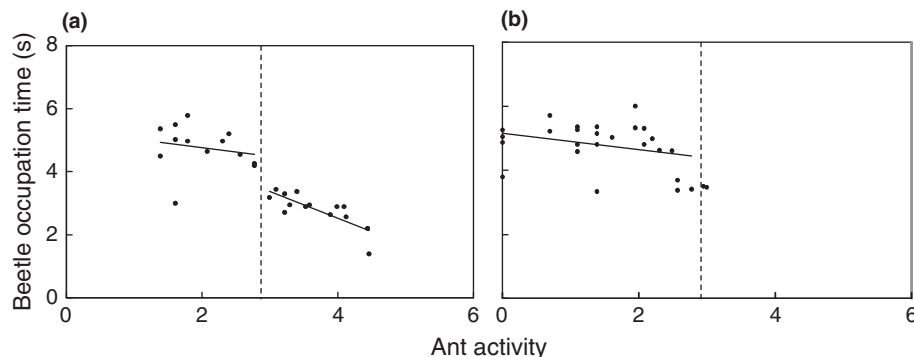


Figure 3. Ant activity effect on beetle occupation time (in seconds) in coffee bushes. Both axes in log ($x + 1$) scale where a value of 2.77 corresponds to the threshold of 15 ants min^{-1} . (a) Relationship between ant activity and beetle occupation time before phorids arrived. The dashed line indicates the threshold below which beetles appear not to be affected by ant activity ($R^2 = 0.0192$, $p > 0.05$, $n = 13$). Above the threshold there is a strong significant negative relationship ($R^2 = 0.627$, $p < 0.005$, $n = 14$). (b) Relationship after phorids arrived to the plant. Ant activity was mostly reduced below the threshold where beetles are not disturbed ($R^2 = 0.09$, $p > 0.05$, $n = 25$).

Discussion

Trait-mediated interactions are ubiquitous in ecological communities (Preisser et al. 2005), and the potential for behaviorally driven trophic cascades appears similarly widespread (Peacor and Werner 2001, Schmitz et al. 2004). Though TMIs in tri-trophic interactions have been well studied, few empirical studies have looked how multiple interacting TMIs are transmitted throughout a community (but see LeBrun and Feener 2002). Here we show such a system in which through the first trait-mediated interaction, *A. instabilis* ants protect their scale insect partners by non-lethally harassing the predatory ladybeetles forcing them to abandon the scale-infested coffee bushes. These patrolling and foraging activities sometimes attract a parasitic phorid fly which causes *A. instabilis* to seek shelter or alter their behavior in a way that renders them incapable of effectively harassing the predatory ladybeetles, thus the second TMI. Similar to LeBrun and Feener (2002) who showed that two interacting TMIs could be important in explaining the structure of ant assemblages, here we show how a cascade of trait-mediated interactions can have strong effects on the dynamics of a biological community.

Our results show that, in the absence of ant-attacking parasitoid flies, the *A. instabilis* – *C. viridis* association works like any other ant–hemipteran mutualism (Way 1963). As expected, in our laboratory experiments, fewer scales were killed in the presence of tending ants, and accordingly in the field, ant harassment reduced the time ladybeetles were able to stay in scale-infested plants, presumably reducing their foraging capability. Thus, we showed that *A. instabilis* tend their mutualistic partners and provide them enemy-free space against predatory ladybeetles. Additionally, despite the fact that we never observed any beetle being caught or killed by ants either in the field or in the lab, ant patrolling did effectively reduce the number of scales eaten, suggesting that the interaction by which the ants provide enemy-free space to their mutualistic partners is indeed indirect and trait-mediated.

The impact of TMIs on non-trophic interactions, like mutualisms, has received much less attention than their

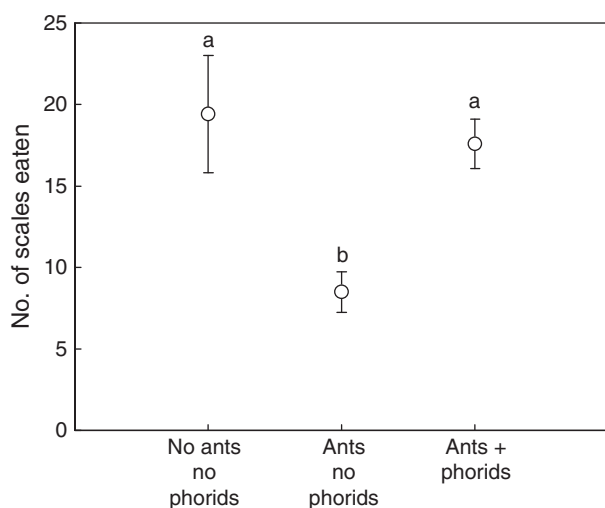


Figure 4. Effect of phorid flies (*Pseudacteon* sp) on the protection given by *Azteca instabilis* to their mutualistic scale partners, *Coccus viridis*, against predation from the ladybeetle *Azya orbigera*. Experiments were conducted in the lab inside rearing cages ($n = 14$). Figure shows mean adult scales eaten in 24 h \pm SE. Different letters indicate statistically significant differences between treatments (post-hoc Tukey test, $p < 0.005$).

influence on trophic interactions (Bronstein and Barbosa 2002). Traditionally, mutualisms have been studied as pairwise interactions, and the fact that they are embedded within complex ecological communities, and that the effect that the mutualistic partners have on one another might be context-dependent, has only recently been recognized (Bronstein 1994, Holland et al. 2002, Stanton 2003). It is known that the outcome of mutualistic associations is not necessarily stable and that due to biotic or abiotic conditions the net effect of species on each other can vary in space and time. Thus, a mutualistic association can vary from strong mutualism, to weak mutualism, to commensalism, and even to antagonism depending on the circumstance (Bronstein 1998, Stanton 2003). For example, in an ant–hemipteran mutualism, both partners gain a benefit from the association: ants gain a direct benefit in the form of honeydew, and scales gain an indirect and behaviorally driven benefit in the form of enemy-free space (Way 1963, Beattie 1985). However, our results show how the outcome of this trait-mediated association can be altered. In the absence of parasitoids, beetles were usually forced off plants and prevented from preying upon ant-tended scales; conversely, when phorids were present, ants were forced to reduce their activity levels leaving beetles undisturbed to freely prey upon the scales. Therefore, while presumably the scale insects continued producing honeydew, the presence of the parasitoids rendered ants unable to effectively harass the predators of their mutualistic partners. Consequently, our results suggest that through a cascade of trait-mediation, the association between ants and scales might alternate between mutualistic and antagonistic based on phorid presence.

The importance of this cascade of indirect interactions depends on whether or not phorids have persistent effects on the ants so as to be consequential for the community dynamics. In general, phorid flies' ability to significantly

affect ant populations has been extensively studied due to its potential as biological control of imported fire ants (Jouvenaz 1983, Feener and Brown 1992, Porter et al. 1995, Morrison et al. 2000, LeBrun and Feener 2002, Mehdiabadi and Gilbert 2002). In our particular system, phorids also have a great potential to significantly impact *A. instabilis* populations. Previous studies on the area (Philpott et al. 2004, 2009, Philpott 2005) as well as personal observations suggest that wherever phorids are present, they are active throughout the day and will attack ant colonies when ants become agitated. While defending their territory, ants release pheromones which act as attractants to nearby parasitoids (Mathis et al. unpubl.). Consequently, if phorids are in the area, they will launch attacks, which can diminish *A. instabilis* competitive abilities (Philpott et al. 2004, Philpott 2005). Similarly, phorid presence could cause persistent changes in the ant–beetle–scale interactions and the results of our laboratory experiments could well represent what is happening in the field.

It is well known that local community interactions can cause unexpected spatial patterns (Hassell et al. 1991, Rohani et al. 1994, 1997). Consequently, cascades of trait mediation could potentially influence the spatial distribution of the organisms in the community. Our data demonstrate that *A. instabilis* greatly reduces the foraging ability of *A. orbigera* and therefore, it would be expected that these beetles would be forced to only prey upon the smaller, unprotected scale populations present throughout the farm in areas without colonies of *A. instabilis*. However, we have observed that the ladybeetles, both as larvae and as adults, are highly concentrated around *A. instabilis* nests (Liere unpubl.). Thus their distribution, as well as the ants', is highly clumped (Vandermeer et al. 2008). We suspect that the presence of phorid flies and their effect on ant activity might explain this counterintuitive spatial pattern. Since adult beetles usually remain within a limited distance of scale-infested plants and repeatedly return to these plants even after being harassed and forced to fly away (Liere unpubl.), they might opportunistically forage in these high prey-density areas when phorids force ants to suspend their tending behavior. These interactions could potentially explain the aggregated distribution of these ladybeetles around ant nests.

Potentially the most persistent effect of the phorid-induced change in ant behavior may be the ability of the ladybeetle to capitalize on the low ant-activity periods to oviposit in ant-tended plants. Due to waxy filaments that cover their bodies and render them immune to ant attacks, *A. orbigera* larvae benefit greatly by living in close association with ants via access to a persistent and abundant food supply and enemy-free space (Liere and Perfecto 2008). Consequently, ovipositing in ant-patrolled plants represents a great fitness advantage for females. However, oviposition might be too difficult and risky under constant ant patrolling since similar to other ladybird beetles (Kawauchi 1985, Nais 2008), *A. orbigera* oviposits under scale exuvia or carcasses to protect their fragile eggs from predation. Thus, they have to be able reach the branches with scales, locate the exuvia or dead scales and lift them to oviposit underneath; a lengthy process that might only be possible during the phorid-induced low ant-activity periods. Even though our experiments tested only for the effects of phorid flies on the foraging efficiency

of the beetles, given the nature of the oviposition behavior of the beetles, we suggest that phorid-induced low ant-activity periods also provide excellent opportunities for the adult ladybeetles to oviposit in these high-quality areas. Thus, a chain of interacting TMII might very well explain the counterintuitive spatial distribution of ladybeetles, and may in fact enable the persistence of the beetle at higher densities than would otherwise be feasible based on the sparse scale populations existing outside of ant-tended plants. Though more research is necessary to confirm these predictions, it seems clear there exists community wide effects stemming from the phorid-ant interaction.

Furthermore, these local interactions might determine the spatial dynamics of ant nests in the area. When beetles attempt to prey upon ant-tended scales, they usually trigger *A. instabilis* attacks. This agitation may attract nearby phorids, which in turn, may force ants to reduce their activity levels long enough for the beetles to oviposit or prey upon scales. Consequently, high phorid abundance around an ant colony could render ants largely incapable of defending their mutualistic partners, whose populations in the area could thus be easily decimated. Without their main carbohydrate source, the ant colony would be forced to move to another tree or face starvation, which corresponds with the high ant nest mortality and turnover in the farm (Vandermeer et al. 2008). Moreover, since ant-nest cluster size is positively correlated with phorid densities (Vandermeer et al. 2008) phorid-induced nest mortality and movement might be stronger in areas with high concentrations of ant nests.

Similar interactions have been recorded in an ant-plant mutualism where in the presence of spiders, patrolling ants sought refuge and suspended their tending behavior leaving their mutualistic plants unprotected against herbivory (Gastreich 1999). Since biological communities are complex networks of interactions, cascading trait-mediations most likely extend outside ant-hemipteran or ant-plant mutualisms and might be a feature in most systems. We believe that more attention should be paid to this type of cascade and that questions related to the extent and strength of these interactions in structuring ecological communities should be addressed. By answering these questions, we might be able to gain a better understanding of context-dependent community interactions and be able to explain counterintuitive and unexpected spatial or temporal patterns.

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