Taking trophic cascades up a level: behaviorally-modified effects of phorid flies on ants and ant prey in coffee agroecosystems

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Trophic cascades exist in numerous terrestrial systems, including many systems with ants as the top predator. Many studies show how behavioral modifications of herbivores are especially important in mediating species interactions and trophic cascades. Although most studies of trophic cascades focus on predator-herbivore-plant links, the trophic cascades concept could be applied to almost any level of trophic interactions. Especially considering the importance of parasites we consider here the interactions between the parasitic phorid fly, *Pseudacteon* sp. (Diptera: Phoridae), its ant host, *Azteca instabilis* (F. Smith) (Hymenoptera: Formicidae), and the herbivore, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) in the coffee agroecosystem. We investigated the effects of phorid flies on ant behavior by monitoring ant recruitment to tuna baits over a 30-min period in the presence or absence of phorid flies. To study the indirect effects of phorids on larvae, we placed baits on coffee plants to elevate ant foraging levels to levels near to ant nests, placed larvae near baits, and recorded the effects of ants on larvae either in the presence or absence of phorid flies. We found that phorid fly presence significantly reduced ant ability to recruit to baits through behavioral modifications and also significantly lessened ant ability to attack, carry away, or force herbivores off plants. We conclude there is a behaviorally-modified species-level trophic cascade in the coffee agroecosystem, with potentially important effects in ant and herbivore communities as well as for coffee production.

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Trophic cascades exist in many terrestrial ecosystems (reviewed by Schmitz et al. 2000). Not surprisingly, many terrestrial cascades involve ants as top predators. For example, ants exhibited "top-down" effects in 25 of 41 studies examined by Schmitz et al. (2000) by namely affecting herbivore communities and aspects of plant growth and reproduction in various ecosystems. Perhaps due to the seemingly wide-spread occurrence of these terrestrial cascades, Polis (2000) separated trophic cascades into two distinct categories: 1) species-level

cascades where changes in predator numbers influence the success of one or a few herbivores and one or a few plant species and 2) community-level cascades where similar changes in predator numbers affect the distribution of total plant biomass within a given system.

One way in which trophic cascades may form is via behavioral or trait-meditated indirect interactions (TMII, Schmitz et al. 2000). TMII occur when a predator influences changes in the behavior or a trait of a prey, with subsequent changes in prey growth or

survival, or changes in competitive interactions between multiple prey species (Werner 1991, 1992, Werner and Anholt 1996, Peacor and Werner 2001). Specifically, many studies highlight ant-modifications of herbivore behavior and subsequent effects on plants (Messina 1981, Way and Khoo 1992) ultimately resulting in the formation of behaviorally-mediated trophic cascades (Schmitz et al. 2000). Furthermore, behaviorally-mediated effects are sometimes equal to or stronger than density-mediated effects whereby predators actually kill prey items (Schmitz et al. 1997, Peacor and Werner 2001).

Parasites are often ignored in studies of food webs (Marcogliese and Cone 1997) and of trophic cascades, even though they have strong community and trophic level effects (Marcogliese and Cone 1997, Feener 2000), but the biological control literature is full of examples of how parasitoid wasps and flies influence agricultural systems (DeBach 1974). Examples cover both the positive effects that parasitoid flies and wasps can have on agricultural crops via their interactions with crop pests (DeBach 1974) as well as negative effects when an introduced biological control agent has strong unanticipated effects on agricultural or neighboring arthropod or plant communities (Secord and Kareiva 1996, Simberloff and Stiling 1996, Schellhorn et al. 2002).

Parasitoid phorid flies affect ants directly via mortality and indirectly via behavioral modifications (Disney 1994). Among the best-studied examples of phorid-ant interactions include *Pseudacteon* spp. (Diptera: Phoridae) flies attacking fire ants (*Solenopsis invicta*) (Buren) (Hymenoptera: Formicidae). Phorid flies parasitize fire ants by laying eggs in ant bodies where larvae and pupae develop thus killing their ant hosts (Feener 2000, Consoli et al. 2001). Even more commonly, phorid flies affect the behavior of their hosts by limiting ant foraging and food acquisition behaviors (Feener and Brown 1992, Porter et al. 1995, Folgarait and Gilbert 1999, Feener 2000, Wuellner et al. 2002), and these effects may be of greater magnitude than direct effects (Feener 1988, Morrison 1999). As a result of ant behavioral changes, phorid flies may mediate changes in competitive interactions between host ants and co-occurring ant species not attacked by phorid flies, perhaps ultimately determining ant assemblages (Morrison 1999, 2000, Morrison et al. 2000, Feener 2000, LeBrun and Feener 2002).

Coffee (*Coffea arabica*) (L.) (Rubiaceae) is a tropical agroforest crop traditionally grown under a shade canopy and supporting much biological diversity. For this reason, its importance for the conservation and preservation of arthropod and bird diversity has attracted much attention (Perfecto and Snelling 1995, Johnson 1996, Perfecto et al. 1996, Greenberg et al. 1997a, 1997b, Moguel and Toledo 1999). Although many studies have examined food web interactions in agricultural systems, primarily in the vast literature on

biological control, these studies are often ignored in reviews of trophic cascades (Schmitz 2000) because of the presumed simplicity of agroecosystems. Here we argue that because tropical agroecosystems, and in particular coffee agroecosystems, host high levels of biodiversity at times comparable to tropical forests, coffee systems potentially host complex food webs (see Vandermeer et al. 2002) and trophic cascades.

In this study, we examine a possible species-level trophic cascade functioning via behaviorally-mediated effects of a phorid fly (an undescribed species of *Pseudacteon*, B. Brown, pers. comm.) (Diptera: Phoridae) on ant hosts (*Azteca instabilis*) (L. Smith) (Hymenoptera: Formicidae) and subsequent indirect positive effects on herbivores (*Spodoptera frugiperda*) (J.E. Smith) (Lepidoptera: Noctuidae) in the coffee agroecosystem. We specifically tested the hypotheses that 1) Phorid flies modify the behavior of their *Azteca* ant hosts reducing ant recruitment (cooperative foraging behavior) and 2) Phorid flies, via their negative influences on ants, have indirect positive effects on ant prey, creating a species-level trophic cascade. Thus, we wish to examine if a tri-trophic cascade operates between phorid flies, ants, and ant prey. We also examine the potential effects that phorid flies may have on ant and herbivore communities, and ultimately on coffee production.

Methods

We conducted our study in two coffee farms in the Soconusco Region of SW Chiapas, Mexico (Finca Irlanda and Finca Belen) in the wet season of 2002 from July to September. Both farms are organic-shaded plantations located 950–1200 m above sea level, located approximately 11 km apart.

To investigate our first hypothesis and to understand how phorid flies affect ant behavior, we examined phorid effects on ant recruitment. We placed food resources (tuna baits) on shade trees with *Azteca instabilis* and recorded ant recruitment to baits. We also noted phorid fly presence at tuna baits. Every 2 min for a total of 30 min, we counted total number of ants at each of 5 baits per shade tree with phorids (N = 130) or without phorids (N = 109). To determine statistical differences between ant recruitment on trees with and without phorids, we compared ant numbers across the 30 min time interval using repeated measures ANOVA with phorid presence and site as between-subject factors.

To investigate possible cascading indirect effects of phorid flies on ant prey, we examined the interaction between ants and lepidopteran larvae with and without phorids. On coffee plants abutting trees with *Azteca* nests, ant activity is high, with several ants per second passing a particular spot on the plant, but as distance from nests increases, *Azteca* activity decreases

(S. Uno, pers. comm.). In order to use both coffee plants adjacent to trees with nests, and other coffee plants further from nests, thus with lower numbers of *Azteca* foragers, we first placed tuna baits on coffee plants to elevate ant activity to a constant level (resembling that of foraging trails un un-baited coffee plants adjacent to trees with *Azteca* nests). We placed up to five baits on each coffee plant used, spaced at least 40 cm from one another. We then sequentially placed individual larvae on coffee leaves or branches near tuna baits (Vandermeer et al. 2002) waiting at least five minutes between baits. Each bait was used only once. Coffee herbivores, although diverse, are relatively not abundant in our field site (S. Philpott, pers. obs.), so we used introduced larvae. For all trials, we used medium sized (5 mm) larvae of *Spodoptera frugiperda*, primarily a corn pest, raised in the laboratory. Although *S. frugiperda* do not naturally occur in coffee systems, ants prey upon *S. frugiperda* in other natural systems (Perfecto 1991, Perfecto and Sediles 1992, Fuller et al. 1997, Eubanks 2001). We then observed interactions between ants and larvae for a maximum of 15 min and recorded for each observation if phorids were present or not. We categorized interactions in the following three ways, after which we ended observations: 1) ants carried larvae away, 2) ants forced larvae off plants, or 3) ants had no effect on larvae (15 min maximum). For the first two categories, statistical differences were determined with univariate ANOVA tests, using phorid presence and site as factors. Differences with phorid presence where ants had no effect on larvae were determined using chi-square tests.

Results

Phorid flies significantly affected ant behavior by reducing ant recruitment and limiting ant abilities to negatively influence ant prey. In terms of ant recruitment, phorid flies significantly lowered number of ants recruiting to baits (Fig. 1). Ant abundance in the presence of phorids was generally less than half of that in the absence of phorids showing a significant impact of phorid presence on ant foraging (repeated measures ANOVA, $P < 0.001$, $F = 21.667$, $df = 1,235$). There were not significant differences between sites (repeated measures ANOVA, $P = 0.335$, $F = 0.932$, $df = 1, 235$), but there was a significant interaction between phorid presence and site (repeated measures ANOVA, $P = 0.039$, $F = 4.310$, $df = 1, 235$). Nonetheless, phorids had significant negative effects on ant behavior in each site (repeated measures ANOVA, Irlanda, $P = 0.048$, $F = 3.979$, $df = 1, 140$; Belen, $P < 0.001$, $F = 19.820$, $df = 1, 95$). Furthermore, there were significant interactions between time and phorid presence (repeated measures ANOVA, $P < 0.001$, $F = 3.726$, $df = 15, 221$).
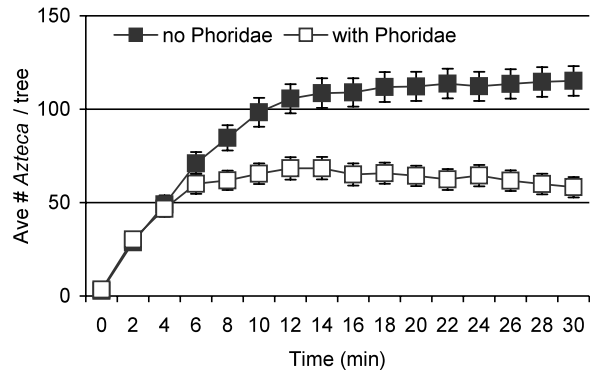

Fig. 1. *Azteca instabilis* ant recruitment with ($N = 130$) or without *Pseudacteon* phorid flies ($N = 109$). Phorids significantly reduced ant ability to forage and thus recruit to tuna baits on shade trees in coffee farms (repeated measures ANOVA, $P < 0.001$, $F = 21.667$, $df = 1, 235$). Bars represent standard error, and patterns did not differ significantly between Finca Irlanda and Finca Belen.

We thus used multivariate ANOVA including each time interval as a dependent variable and phorid presence and site as fixed factors to examine phorid effects at each time interval. Phorids significantly restricted ant recruitment for all time intervals after 6 minutes (Table 1). Thus, in general, phorid flies consistently and drastically limited ant recruitment, likely restricting their overall resource-acquisition abilities and any interactions with prey through behaviorally-mediated interactions.

Phorid flies also had strong positive effects on larvae indirectly via their negative effects on ants. *Azteca* ants reacted to *Spodoptera frugiperda* larvae in one of 3 ways: 1) carrying larvae away ($N = 90$), 2) forcing larvae off plants ($N = 86$), or 3) having no effect on larvae ($N = 9$) (Fig. 2). Importantly, ants did not affect larvae only when phorid flies were present ($N = 9$), and larvae never escaped effects of ants when phorids were absent ($N = 0$) (chi-square test, $P = 0.004$, $df = 1$). In trials where ants did negatively affect larvae, phorid flies significantly slowed interactions. The amount of time for which it took ants to successfully carry away larvae or force larvae off plants was significantly greater in the presence of phorids (Fig. 2). It took on average more than twice as long for ants to carry away larvae (ANOVA, $P = 0.033$, $F = 4.720$, $df = 1, 82$), and although sites differed significantly, in terms of length of time required to affect larvae, there was no significant interaction between phorid presence and site ($P = 0.486$, $F = 0.491$, $df = 1, 82$). Ants were also slower to force larvae off plants ($P = 0.006$, $F = 8.092$, $df = 1, 86$) when phorids were present, and again there were significant differences by site, but not significant interactions between site and phorid presence ($P = 0.169$, $F = 1.921$, $df = 1, 86$).

Table 1. Multivariate ANOVA results showing the effects of *Pseudacteon* phorid flies on *Azteca instabilis* ant recruitment over a 30 min trial period in two different coffee agroecosystem sites. For each time interval after six minutes, phorids had a significant negative effect on ant recruitment.

| Minute	Phorid presence			Site			Phorid presence × site		
	F	P	df	F	P	df	F	P	df
0	0.661	0.417	3, 235	0.001	0.977	3, 235	0.903	0.343	3, 235
2	0.046	0.830	3, 235	0.992	0.320	3, 235	0.511	0.475	3, 235
4	0.382	0.537	3, 235	0.390	0.533	3, 235	2.324	0.129	3, 235
6	2.682	0.103	3, 235	0.051	0.821	3, 235	3.734	0.055	3, 235
8	8.612	0.004	3, 235	0.209	0.648	3, 235	3.903	0.049	3, 235
10	14.092	0.001	3, 235	0.665	0.415	3, 235	5.507	0.020	3, 235
12	16.763	0.001	3, 235	0.666	0.415	3, 235	5.350	0.022	3, 235
14	18.567	0.001	3, 235	1.103	0.295	3, 235	4.821	0.029	3, 235
16	22.228	0.001	3, 235	1.750	0.187	3, 235	2.828	0.094	3, 235
18	23.732	0.001	3, 235	2.630	0.106	3, 235	3.016	0.084	3, 235
20	26.211	0.001	3, 235	1.473	0.226	3, 235	2.990	0.085	3, 235
22	29.644	0.001	3, 235	1.993	0.159	3, 235	3.296	0.071	3, 235
24	25.982	0.001	3, 235	2.097	0.149	3, 235	3.365	0.068	3, 235
26	30.182	0.001	3, 235	0.867	0.353	3, 235	3.663	0.057	3, 235
28	33.935	0.001	3, 235	0.992	0.320	3, 235	4.279	0.040	3, 235
30	36.649	0.001	3, 235	1.602	0.207	3, 235	4.210	0.041	3, 235
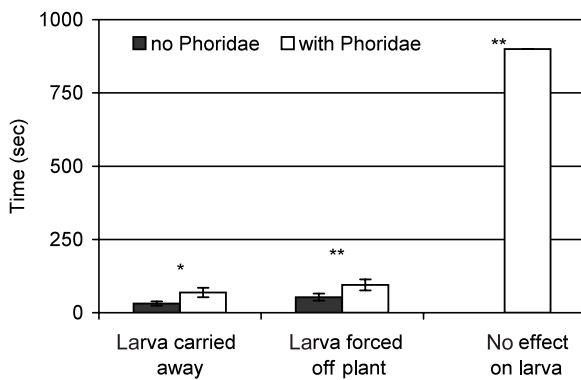
Fig. 2. *Azteca instabilis* ant interactions with *Spodoptera frugiperda* larvae with or without *Pseudacteon* phorid flies. The length of time it took ants to either carry away (ANOVA, $P = 0.033$, $F = 4.720$, df = 1, 82) or force larvae off coffee plants (ANOVA, $P = 0.006$, $F = 8.092$, df = 1, 86) were both significantly increased when phorid flies were present. Only in trials with phorid flies did ants have no effect on larvae (chi-square test, $P = 0.004$, df = 1). Sample sizes were: 1) with phorids (force off plant = 16, carry away = 14, no effect = 9), 2) without phorids (force off plant = 56, carry away = 43, no effect = 0). Bars represent standard error and asterisks show significant differences between with or without phorids.

Discussion

Here, we demonstrate strong effects of phorid flies on ant prey via their interactions with ants. These effects show the potential for the existence of a behaviorally-mediated species-level trophic cascade in the coffee agroecosystem. Phorid fly presence significantly decreased *Azteca* ant recruitment consistent with our first hypothesis. Additionally, we showed that only in the presence of phorid flies did ants have no effect on introduced larvae, and furthermore, ants were significantly slower in killing or removing larvae from coffee plants when phorids were present, consistent with our second hypothesis. Though some larvae were not directly killed by ants, harassment of larvae (i.e. forcing larvae off plants) can effectively reduce larvae populations due to lower feeding rates or increased mortality (Schmitz et al. 1997).

Although in this particular study, we document a species-level trophic cascade connecting *Pseudacteon* phorid flies, *Azteca instabilis* ants, and an introduced prey, *Spodoptera frugiperda*, phorid flies may have much wider influences in coffee agroecosystems, potentially affecting interactions of *Azteca* ants with herbivore communities as well as other ant species. The same genus of phorid fly (*Pseudacteon* sp.) attacks *Solenopsis* spp. fire ants, affecting ants primarily via behavioral modifications (Feener and Brown 1992, Porter et al. 1995, Folgarait and Gilbert 1999, Feener 2000, Wuellner et al. 2002). These behavioral modifications reduce the competitive effects of fire ants on other ants, and presumably limit the secondary effects of fire ant invasion (Orr et al. 1995, Porter and Alonso 1999, Porter et al. 1999). Fire ants, in particular, have disastrous effects in their introduced range, disrupting some biological control methods (Eubanks 2001), and in general interfering with native food webs (Vinson 1994, Wojcik et al. 2001). Many suggest, however, that phorid flies may be effective biological control agents of fire ants (Feener 1981, Feener and Brown 1992, Orr et al. 1995, Porter and Alonso 1999, Porter et al. 1999) perhaps due to the strong behaviorally-mediated effects of phorid flies on ant and arthropod communities. This recommendation suggests that influences of phorid flies on fire ants are strong enough to limit the secondary effects of ant invasion by changing fire ant interactions with and influences in native ant, arthropod and plant communities thereby forming trophic cascades.

144

Using the phorid fly-fire ant system as a model, we propose that phorid flies may have much more widespread effects in the coffee food web, possibly even translating into ramifications at a fourth trophic level – the coffee plants. Here, we show a species-level trophic cascade where a "top-down" influence of phorid flies causes changes in one species of herbivore. Phorid flies, however, may also strongly affect competition in ant communities, as well as other members of the arthropod community and plants.

Azteca instabilis is a numerically dominant ant in the coffee agroecosystem in our study area, but phorids may strongly influence their interactions with other ants. *Azteca* ants are often cited as important in ant mosaics, whereby interspecific competition maintains a spatial division between dominant and sub-dominant ant species (Majer 1972, Leston 1978, Adams 1994). *Azteca* ants in the coffee system we study appear to be competitively dominant over other common ants (*Camponotus senex* and *Crematogaster* spp., S. Philpott, unpubl.). Especially because we have never seen phorids attacking non-*Azteca* ants, phorids may be limiting the total dominance of *A. instabilis* in the system, as Feener (2000) suggests may be happening with other competitively dominant ants in other systems. We have no evidence that *A. instabilis* are limited by resources (i.e. food, nesting sites, etc.), so phorids may be exerting strong local control on *Azteca* ants. Removing phorids from the system entirely could cause a drastic change of the ant community, with subsequent effects in lower trophic levels.

Furthermore, although we highlight the effects of *Azteca* on only *Spodoptera frugiperda* larvae in this particular study, informal observations and other studies in our study sites confirm the findings that *A. instabilis* ants rapidly and effectively attack any naturally occurring or introduced larvae with which they come in contact, often significantly faster than other dominant ant species (Vandermeer et al. 2002, S. Philpott, unpubl., S. Uno, pers. comm.). Le-Pelley (1973) reported that nearly 200 species of herbivores (i.e. potential pests) feed on coffee plants. Ants are important predators in many agroecosystems (Way and Khoo 1992, Perfecto and Castiñeiras 1998), including other tropical agroforestry systems such as cacao (Khoo and Ho 1992, See and Khoo 1996), and thus may be acting to limit the populations of known coffee herbivores. Since phorid flies limit *Azteca* ant foraging and predatory abilities, phorids also indirectly benefit herbivores (possible coffee pests), and thus may negatively affect coffee. Furthermore, many coffee agroecosystems in Chiapas have a large diversity of shade trees (Soto-Pinto et al. 2002). *Azteca instabilis* ants nest mostly in shade trees, and phorids thus might have effects on other plants in this managed, relatively simple plant community. By virtue of the strong effects of phorids on ants and ant prey, and

the known phorid-mediated interactions among ants and on lower trophic levels, the potential exists in this system for a 4-trophic level community cascade between phorids-ants-herbivorous ant prey-and plants.

Despite the potential effects of phorids to create a trophic cascade in coffee agroecosystems, there are several factors by which community-wide effects of phorids may be limited. Phorid flies are active only during the day and ants attacked by phorid flies may show increased foraging activity during the night (Orr et al. 2003, Wuellner and Saunders 2003). Certainly such changes in activity levels will have impacts on the refuge phorids provide for herbivores. Little is known about the night-time activity levels of *A. instabilis* ants in particular, but it is possible that ant predation rates on larvae may be greater during the night thus lessening the protective effects of phorids on ant prey. Furthermore, although ant densities may not correlate with phorid densities (Morrison et al. 2000), there may be some threshold activity level of ants required to attract phorid flies. Although we have seen phorids attacking ant colonies at natural densities (i.e. without the use of baits or other disturbances to ant nests) ants at very low densities may escape phorid notice, with important implications for ant prey. Furthermore, if *Azteca* activities are naturally highest near a nest, and diminish with distance away from the nest, the effects of phorid flies on ants and ant prey may be greater near nests where activity levels naturally surpass thresholds and lower further away from nests where activity levels are potentially not high enough to attract phorids. Because we used tuna baits to elevate activity on all coffee plants to resemble levels close to nests, our results do not necessarily address this interesting spatial component nor how phorid effects may change with ant densities.

In conclusion, phorid flies strongly affected *Azteca* ant behavior, and also significantly limited *Azteca* abilities to attack *Spodoptera* larvae showing the potential for a species-level trophic cascade in the coffee agroecosystem. It is possible that phorid flies may have more widespread effects in the coffee agroecosystem, affecting ant competition, herbivore communities, and potentially influencing shade trees and coffee plants thus creating a community-level trophic cascade. The ultimate effects of phorid flies in the coffee agroecosystem, however, will also depend on temporal and spatial changes in phorid-ant interactions as well as how effects of phorids change with ant densities.

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