Behavioral Diversity of Predatory Arboreal Ants in Coffee Agroecosystems

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ABSTRACT Aspects of predator assemblages that alter predator effects on prey have received extensive recent attention. Among other mechanisms, differences in behavior or resource use within predator trophic levels may enhance predator effects on prey, especially if effects of each predator species differ with environmental conditions. We address whether three common ant species (*Azteca instabilis* F. Smith, *Camponotus textor* Forel, and *Crematogaster* spp.) are functionally unique in coffee agroecosystems, asking if each species differs in (1) cooperative foraging behavior, (2) responses to experimentally introduced herbivores, and (3) responses to pest outbreaks. Furthermore, we examined the behaviors and effects of each ant species under different conditions by varying herbivore species, herbivore size, and herbivore density and carrying out observations in different seasons. Ant species significantly differed in foraging behaviors, in effects on individual herbivores, and in responses to pest outbreaks in terms of both type and time of response to herbivores. The behaviors and effects of each ant species differed in the dry and wet seasons and for different herbivore species and sizes. Although *A. instabilis* generally removed more larvae and more quickly removed larvae, this was not the case under all conditions. The data presented thus support that common ant species in coffee agroecosystems are behaviorally diverse in their responses to herbivores under different conditions. We discuss the implications of these differences in ant behaviors for enhancement of predatory function in light of both multipredator effects and in terms of the potential importance of predator diversity.

KEY WORDS resource partitioning, multipredator effect, intraguild predation, trophic interaction, Chiapas, Mexico

Much recent work has focused on what components of predator assemblages may alter their potential impacts on prey communities. Historical divisions in the literature on multiple predator effects on the one hand, and the biodiversity and ecosystem function literature on the other, have been drawn together in recent syntheses (Ives et al. 2005, Casula et al. 2006). This rich literature has resulted in a number of different proposed mechanisms for why predator effects differ. Because it is often the case in predator communities that one predator is more efficient than others, presence of such species (especially likely in diverse predator assemblages) may result in greater effects on the whole (Hooper et al. 2005, Ives et al. 2005). Interactions between predators and prey may also strongly influence top-down effects. Intraguild predation or competition between predators may negatively affect overall predatory effects, especially where there is a strong asymmetry such that some predators feed almost exclusively on other predators (Finke and Denno 2004, Ives et al. 2005). In contrast, it is possible that competitive interactions between predators may result in phenotypic niche shifts whereby predators collectively extend (rather than reduce) their prey resource base in the presence of other species relative to when preying alone (Casula et al. 2006). Predator effects may also be nonadditive if predators induce behavioral responses (defense or otherwise) of prey that increase capture rates by another predator species (Sih et al. 1998, Ives et al. 2005). Perhaps the area that has received the least empirical attention in the predation literature is resource partitioning by predators. In the context of multipredator effects, resource partitioning may mean that each predator consumes different species, sizes, and or life-stages of prey assemblages such that overall predator effects on the prey biomass are enhanced (Duffy et al. 2003, Ives et al. 2005). Additionally, differential use of resources are expected to be even more important if there is a high level of spatial or temporal variation in the predator assemblage or in predator habitat use (Sih et al. 1998, Cardinale et al. 2004, Loreau 2004, Dimitrakopoulos and Schmid 2004). Thus, understanding differences in both spatial and temporal variation in predator behavior and resource uses is important. As more theory and empirical work emerges, it is increasingly clear that multiple predator presence

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can increase or decrease effects on prey assemblages and that the underlying mechanisms are very complex.

Ants are important generalist predators in many natural and agricultural systems (Way and Khoo 1992, Perfecto and Casteñeiras 1998, Schmitz et al. 2000). Ants attack herbivores using many different strategies including direct predation, chemical deterrence, or by forcing them off plants (Way and Khoo 1992, Vandermeer et al. 2002). Several lines of evidence from ant communities indicate that the predatory effects on prey assemblages may be enhanced when multiple predators are present. First, some of the classic literature on resource partitioning comes from seed-eating ants that use seeds based on their body size (Davidson 1978). Second, tropical ants in particular are noted for patchy distributions (Room 1975, Leston 1978) likely meaning that the foraging ranges and strata of some important ant species differ significantly. Third, at least one study has previously examined behavioral differences in the responses of ant species to introduced prey finding that one species (*Pseudomyrmex triplarinus* Weddell) attacked more baits and attacked more quickly than the other (*Crematogaster* sp.) (Oliveira et al. 1987). They also found that *Pseudomyrmex triplarinus* attacks were distributed plantwide, whereas *Crematogaster* sp. allocated workers to the lower tree strata. Although the authors did mention that there were some aggressive interactions over prey items, this work did not directly discuss how these behavioral differences and differences in foraging strategies may have influenced overall consumption rates or overall importance of the multiple ant predators.

The importance of ants as predators in coffee agroecosystems is increasingly acknowledged (Philpott and Armbrecht 2006). There are >200 species of herbivores that attack coffee, several of which are important pests (Le-Pelley 1973). It has already been documented that several species of ants prey on the coffee berry borer (*Hypothenemus hampei* Ferrari), and ants reduce densities of lepidopteran larvae in coffee plants (Armbrecht 2003, Perfecto and Vandermeer 2006). Ants also significantly differ in their effects on canopy arthropods in coffee agroecosystems (Philpott et al. 2004a) yet it is unknown how the effects of particular ant species on herbivores differ in the coffee layer. If ant species differentially affect prey, they may have different effects in food webs and may respond differently to changes in environmental conditions. Here, we focus on the predatory roles of different ant species in coffee agroecosystems to study the potential for behavioral differences in foraging and also in responses to prey. Specifically, we studied cooperative foraging behavior (recruitment) and the effects of ants on herbivores experimentally introduced into the coffee system. We included different species, sizes, and densities of herbivores and observations in different seasons as surrogates of changes in environmental conditions.

Materials and Methods

Sites and Natural History. We carried out field studies in two coffee farms in the Soconusco Region of southwest Chiapas, Mexico: (1) Finca Irlanda (15°11′ N, 92°20′ W) and (2) Finca Belen (15°15′ N, 92°22′ W). Both farms cover >200 ha, are organically managed, are located between 950- and 1,150-m elevation, and receive ≈4,500 mm of rain/yr. The areas of the farms in which studies were conducted are managed somewhere between traditional and commercial polycultures (Moguel and Toledo 1999), and have ≈50–70% shade cover.

To examine the foraging behaviors and predatory effects of ants, we concentrated on three numerically dominant ant species: (1) *Azteca instabilis* F. Smith, (2) *Camponotus textor* Forel, and (3) *Crematogaster* spp. Several species of *Crematogaster* occur in the study sites including *C. carinata* Mayr, *C. crinosa* Mayr, *C. formosa* Mayr, *C. nigropilosa* Mayr, and *C. sumichrasti* Mayr. Unfortunately, these were not distinguished during field surveys and thus are treated as a genus here. Post hoc data collection in the same areas indicate that roughly 75% of original observations can be accounted for by *C. crinosa* (≈50%), *C. nigropilosa* (≈15%), and one undetermined species of *Crematogaster* (10%).

Previous work has examined the effects of *A. instabilis* and *C. textor* on herbivores in coffee agroecosystems. Two studies examined the effects of *A. instabilis* on experimentally introduced larvae and on the coffee berry borer, showing that this species effectively and quickly removes herbivores, especially when associated with scale insect patches (Vandermeer et al. 2002, Perfecto and Vandermeer 2006). Furthermore, *A. instabilis* and *C. textor* have significantly different effects on canopy arthropods in the same sites; they have positive and negative effects on different arthropod taxa and also have stronger overall effects in different seasons (Philpott et al. 2004a). With this as a backdrop, we compared the foraging behaviors of *A. instabilis*, *C. textor*, and *Crematogaster* spp. and examined differences in their effects on herbivores (two species, sizes, and densities) experimentally introduced in the wet and dry seasons observing both the type of effect they had on herbivores and the speed with which they responded to herbivore introduction.

Ant Foraging Behavior. To study recruitment, or collective foraging, we haphazardly located shade trees on which the three ants were abundant and placed five tuna baits, ≈5 g each, 1.5 m above ground, on each tree. Shade trees used for observations differed with year and season but included four *Inga* spp. (≈55% of observations), *Alchornea latifolia* Swartz (Euphorbiaceae) (25%), *Quercus* spp. (5%), *Cordia stellifera* I. M. Johnston (Boraginaceae) (5%), and >20 other species accounting for <1% of observations. Tuna, a protein resource, commonly used to sample ant diversity and activity was selected for baits. Every 2 min for 30 min, we recorded the number of ants at baits. We made all observations between 0830 and 1430 hours on several days during three wet seasons

(June/July 2000–2002) and three dry seasons (January/March 2001–2003). We limited observation time to a few hours of the day, excluding dawn and dusk, because ant foraging activity may vary depend on time of day or night. Each tree was used once per season, but some individual trees were used again in different seasons. The number of trees with each ant species used varied from 11 to 42 trees per species per season for an overall total of 108 trees with *A. instabilis,* 111 trees with *C. textor,* and 261 trees with *Crematogaster* spp. A species of phorid fly (*Pseudacteon* sp.) impairs *A. instabilis* recruitment and also limits the ability of this ant to attack larvae (Philpott et al. 2004b). Although this is clearly an important aspect of arboreal ant ecology in the study system, we wanted to here focus the discussion on a comparison of ant species; thus, we removed all trees where phorids were observed (60) from the analysis leaving a total of 48 trees with *A. instabilis.*

We compared ant recruitment using numbers of recruits and rate of change in the number of recruits between two counts. The recruitment rate was calculated as the numbers of ants in time $T + 1 -$ the number of ants at time T. We used repeated-measures analysis of variance (ANVOA) with time as the repeated factor and ant species and season as between-subject factors. We used a subset of repeated measures for each analysis (2, 6, 10, 14, 18, 22, 26, and 30 min) to reduce likelihood of error. Assumptions of sphericity were not met (recruitment numbers, Mauchley's $W = 0$; recruitment rate, Mauchley's $W = 0.554$); therefore, we report Huynh-Feldt corrections to test for significant differences in recruitment by ant taxa (Scheiner and Gurevitch 1993). We determined differences between ant species using Tukey's post hoc tests. For significant interaction terms, we used repeated-measures ANOVA for each factor.

Ant Effects on Herbivores. During the wet and dry seasons of 2002, we experimentally introduced laboratory-raised larvae of *Spodoptera frugiperda* J. E. Smith (Noctuidae) and *Estigmene acrea* Drury (Arctiidae) of two sizes, small (≈2–3 mm) or large (≈5–8 mm), on to haphazardly selected coffee plants with *A. instabilis, C. textor,* or *Crematogaster* spp. We chose larvae of these sizes such that small larvae were smaller than the ants observed, and large larvae were larger than the largest ants observed. Both larval species are native to the neotropics and are graminoid specialists. The species differ in that *S. frugiperda* is a smooth larva, and *E. acrea* is defended by dense hairs. These larvae do not naturally occur in coffee systems, which may have affected the behavior of the larvae, but ants prey on *S. frugiperda* in other natural systems (Perfecto and Sediles 1992). We placed a single larva at least 10 cm from ant foraging trails in coffee plants and observed larvae until they were removed or for a maximum of 15 min. We recorded (1) outcome (i.e., larvae taken by ants, larvae thrown off plants by ants, or no effect) and (2) time it took for ants to remove larvae. Sample sizes varied with availability of larvae and coffee plants with desired ant species. We introduced a total of 294 small larvae (127 on plants with *A. instabilis,* 98 on plants with *C. textor,* and 69 on plants with *Crematogaster* spp.) and large larvae of *S. frugiperda* (119 on plants with *A. instabilis,* 96 on plants with *C. textor,* and 74 on plants with *Crematogaster* spp. We used 111 large *E. acrea* (38 on plants with *A. instabilis,* 41 on plants with *C. textor,* and 32 on plants with *Crematogaster* spp.).

We examined differences between ants in terms of outcome and time it took ants to remove larvae. To examine differences in the frequency of outcomes based on ant species, larva species, and larva size, we used a nominal log-likelihood model in JMP IN 5.1. We included the three outcomes as the dependent variable, frequency as weight, and ant species, species of larva, and size of larva as main factors. Because of limited availability of *E. acrea* from the laboratory, this species was introduced only in the dry season. Season was not included as a main factor in the model, because this effect was not separable from differences attributed to species. We first ran models with full factorial designs, eliminated all nonsignificant higher order interactions, and reran models. To examine differences in how long it took ants to remove larvae, we used ANOVA where time was the dependent variable, and ant species, larva species, and larva size were between-subject factors. We determined pairwise differences using Tukey's post hoc tests. For significant interaction terms, we used repeated-measures ANOVA for each factor.

Ant Response to Pest Outbreaks. In the wet and dry seasons of 2002, we simulated pest outbreaks in coffee plants by adding a high density of *S. frugiperda* larvae (10 larvae per plant) to haphazardly selected plants with *A. instabilis, C. textor,* and *Crematogaster* spp. Background densities of lepidopteran larvae (>25 unidentified species) on coffee plants in the study sites are ≈2.1 larvae per plant (Perfecto et al. 2004). We also placed *S. frugiperda* larvae on plants where ants were excluded by eliminating all dry twig nests and by placing Tanglefoot around coffee trunks. We placed either 10 small or large larvae (sizes as above) haphazardly over all areas of coffee plants (top to bottom, close or far from main trunk) and observed plants continuously for 2 h. For each larva, we recorded (1) outcome and (2) time at which outcome occurred. Outcomes in these trials, in contrast to those with only one larva per plant, included attacks by other ant species (in addition to *A. instabilis, C. textor,* and *Crematogaster* spp.) and also by other predator taxa (i.e., spiders, lizards, predatory wasps). We thus included removal by other ants, and removal by other predator taxa to the possible outcomes. In total, we introduced large larvae onto 30 plants with *A. instabilis,* 32 plants with *C. textor,* 21 plants with *Crematogaster* spp., and 25 plants without ants. We introduced small larvae onto 39 plants with *A. instabilis,* 31 plants with *C. textor,* 25 plants with *Crematogaster* spp., and 8 plants without ants.

To analyze the effects of ants on larvae, we first summed the frequencies of each outcome according to ant taxa, larva size, and season. To examine for differences in these frequencies, we used a nominal

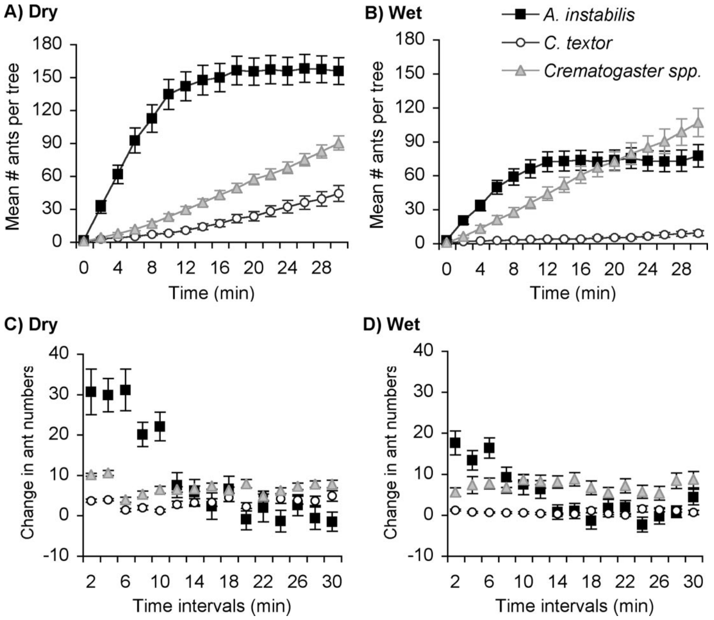

Fig. 1. Recruitment behavior of three ant taxa in to tuna baits on shade trees in coffee agroecosystems. Numbers show number of ant workers recruiting over a 30-min period (A and B) or recruitment rate (change in ant numbers between counts) (C and D). Error bars show SE.

log-likelihood model with JMP IN 5.1. We first ran models with full factorial designs and then reran models with all nonsignificant higher-order interactions eliminated. Plants without ants were only used in one season, so statistical tests of frequencies only included plants with the three ant taxa. Because the frequency of other ant species or other predator taxa removing larvae was very low, we combined this category into one outcome—other predators. We included the four outcomes as the dependent variable, frequency as weight, and ant species, larva size, and season as main factors. We also examined differences in time to larvae removal. We categorized the 2-h period into twelve 10-min time intervals, and calculated on a per plant basis the cumulative number of larvae removed by ants during each time interval. Average numbers of removed larvae per interval, as well as removal rate were analyzed with repeated-measures ANOVA with ant species and season as between-subject factors. We made pairwise comparisons using Tukey's tests and used separate repeated-measures ANOVA to distinguish effects of significant interaction terms. Assumptions of sphericity were not met (removal numbers, Mauchley's W = 0; removal rate, Mauchley's W = 0.053); therefore, we report Huynh-Feldt corrections to test for significant differences in larvae removal by ant species (Scheiner and Gurevitch 1993).

Results

Ant Foraging Behavior. The species of ants examined have significantly different recruitment strategies measured in terms of both numbers of individuals recruited and recruitment rate (Fig. 1; Table 1). Foraging strategy of each species differed significantly, with *A. instabilis* recruiting in higher numbers and initially faster than the other two species ($P < 0.001$). *Crematogaster* spp. recruited at a relatively constant rate, whereas *C. textor* was initially slow and slightly increasing at the later end of the 30 min ($P < 0.001$). *Crematogaster* spp. recruited more ants than *C. textor.* Additionally, the recruitment strategies of each ant significantly differed with season. There were significant interaction terms between ant species, season, and time (minute or time interval; Table 1). *A. instabilis* recruited twice as many ants in the dry season than in the wet season (df = 1, $F = 25.981$, $P < 0.001$), and *C. textor* recruited four times as many workers (df = 1, $F = 23.396$, $P < 0.001$). Numbers of *Crematogaster* spp. did not differ between seasons (df = 1, $F = 3.591$, $P = 0.059$). Additionally, *A. instabilis* recruited more quickly for the first few minutes in the dry season than in the wet season (df = 1, $F = 15.051$, $P < 0.001$), and *C. textor* recruitment rates were consistently higher over the half hour period in the dry season (df = 1, $F = 24.583$, $P < 0.001$). In contrast, *Crematogaster* recruitment rates did not differ with season (df = 1, $F = 2.045$, $P = 0.154$).

Ant Effects on Herbivores. Overall, ants had strong negative effects on herbivores. Ants took away or threw off of plants the vast majority of larvae that were introduced during the 15-min period; *A. instabilis* removed 98.5% of larvae, *C. textor* removed 90.6%, and *Crematogaster* removed 90.3%. The frequency of different outcomes depended on ant species (Table 2). *A. instabilis* took larvae away much more often (33.0% of trials) than did *C. textor* (11.1%) or *Crematogaster* spp. (9.7%), and threw larvae off plants much less

Table 1. Differences in no. recruits and recruitment rate of ants recruiting to baits on shade trees in coffee plantations over 30 min

	df	MS	*F*	*P*
Number of recruits				
Ant species	2	1538166.489	79.136	<0.001
Season	1	388836.063	20.005	<0.001
Ant species × season	2	438720.494	22.571	<0.001
Error (ant species)	474	19436.928		
Time	7	208060.142	208.215	<0.001
Time × ant species	14	35529.269	35.556	<0.001
Time × season	7	10162.487	10.17	<0.001
Time × ant species × season	14	9352.648	9.36	<0.001
Error (time)	3,318	999.257		
Epsilon				0.239
Recruitment rate				
Ant species	2	11502.884	33.085	<0.001
Season	1	5163.992	14.853	<0.001
Ant species × season	2	4490.071	12.915	<0.001
Error (ant species)	474	347.673		
Time	7	3446.264	20.83	<0.001
Time × ant species	14	4694.32	28.373	<0.001
Time × season	7	318.557	1.925	0.071
Time × ant species × season	14	752.245	4.547	<0.001
Error (time)	3,318	165.448		
Epsilon				0.883

Results are for repeated-measures ANOVA examining differences between ant species (*A. instabilis*, *C. textor*, and *Crematogaster* spp.) and season (wet and dry). Number of recruits and recruitment rate differed for each ant species (Tukey's tests, $P < 0.001$). *P* values were adjusted for lack of sphericity (Huynh-Feldt).

often (65.4%) than did *C. textor* (79.5%) or *Crematogaster* spp. (80.6%). The size of larvae also significantly affected the outcome of trials (Table 2). Small larvae were taken away (41.1%) more often than large larvae (4%), and large larvae were thrown off plants more often than small larvae (88.5% and 54.4%). The frequency of outcomes was not affected by herbivore species, and there were no significant interactions between ant species and size or species of herbivore.

Table 2. Results from nominal log-likelihood model used to examine relationships between the frequency of outcomes of ant–larvae interactions (larvae taken by ants, larvae thrown off by ants, larvae removed by other predators, or larvae not removed) and ant species (*A. instabilis* versus *C. textor* versus *Crematogaster* spp.), larva species (*S. frugiperda* versus *E. acrea*), larva size (small versus large), and season (wet versus dry)

One larva per plant			
Whole model test			
Log likelihood	df	χ^2	*P*
121.78429	8	243.5686	<0.0001
Effect Wald tests			
Source	df	Wald χ^2	*P*
Ant species	4	61.006536	<0.001
Species	2	0.764025	0.6825
Size	2	82.12388	<0.001
Ten larvae per plant			
Whole model test			
Log likelihood	df	χ^2	*P*
228.423	21	456.8459	<0.0001
Effect Wald tests			
Source	df	Wald χ^2	*P*
Ant species	6	56.299134	<0.0001
Size	3	9.6420085	0.0219
Ant species × size	6	20.867034	0.0019
Season	3	67.266711	<0.0001
Size × season	3	19.92436	0.0002

Data shown are for separate experiments where larvae were experimentally introduced to plants with ants at two different densities.

Ants differed in how quickly they removed (took or threw away) larvae (Fig. 2; df = 2, $F = 7.311$, $P = 0.001$). Of the three ant taxa, *A. instabilis* removed larvae significantly faster than either of the other two species (Tukey's test, $P < 0.001$), but there was no difference in the time it took *C. textor* and *Crematogaster* spp. to remove larvae ($P = 0.972$). There was also a significant interaction between ant species and species of larva (df = 2, $F = 3.532$, $P = 0.030$). *S. frugiperda* larvae were removed at least twice as fast by *A. instabilis* (df = 2, $F = 17.568$, $P < 0.001$) than by *C. textor* (Tukey's test, $P < 0.001$) or *Crematogaster* ($P < 0.001$), but ant species did not differ in how fast they removed *E. acrea* (df = 2, $F = 1.602$, $P = 0.206$). There was no effect of larvae size on removal times by ants.

Ant Response to Pest Outbreaks. At higher larvae densities, the effects of ants and other factors were much more complex (Fig. 3). Many more larvae were removed on plants with ants (*A. instabilis*, 76.4%; *C.*

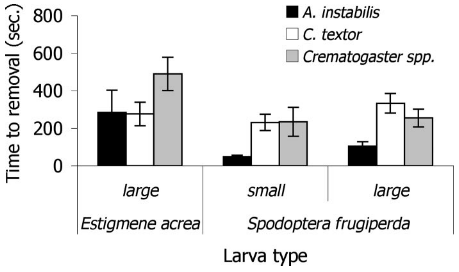

Fig. 2. Times until larvae were removed on coffee plants with one of three ant taxa. Columns show average number of seconds until larvae were either taken away or thrown off plants. Small larvae were ≈2–3 mm and large larvae were ≈5–8 mm. Error bars show SE.

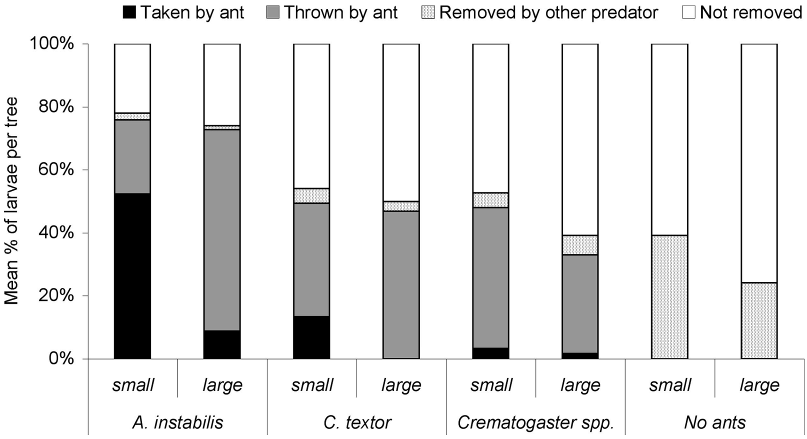

Fig. 3. Frequency of outcomes for *S. frugiperda* larvae experimentally introduced into coffee plants with one of three ant taxa and without ants. Percentages represent average proportions of larvae per tree either removed by ants (taken away or thrown away), removed by other predators (including other ant species and non-ants), or not removed during 2-h trial periods. Small larvae were ≈2–3 mm and large larvae were ≈5–8 mm.

textor, 52.1%; *Crematogaster* spp., 46.7%) than on plants without the three dominant ants (30.4%). Furthermore, on plants without ants, many more larvae were removed by other predators (including other ant species, spiders, predatory wasps, and lizards; 30.4%) than on plants with *A. instabilis* (1.8%), *C. textor* (3.9%), or *Crematogaster* spp. (5.3%). The frequency of different outcomes differed with ant species, larva size, and season and there were significant interactions between ant species and size, and size and season (Table 2). Overall, larvae were taken away more often by *A. instabilis* (35.7%) than the other two ant species (8.0%). On plants with all three ant species, larvae were equally as likely to be thrown off plants or removed by other predators but there were more larvae removed from plants with *A. instabilis* after 2 h (23.5% remained) than on plants with the other ant species (>47% remained). All ants were more likely to take small larvae (28.8%) than large larvae (3.8%). Ants took away more larvae in the wet than in the dry season (28.8% versus 9.7%) and also threw away more larvae in the wet than in the dry season (46.5% versus 28.8%). In the dry season, many more larvae were not removed (53.7%) than in the wet season (19.5%). There was a significant interaction between ant species and larva size ($P = 0.0019$; Table 2); *A. instabilis* and *C. textor* were at least six times as likely to take small (52.3%, 13.3%) than large larvae (8.9%, 0%), whereas *Crematogaster* spp. was less than twice as likely to take small (3.3%) than large (1.7%) larvae. Finally, there was a significant interaction between larva size and season. In the dry season, all ants took more small larvae than in the wet season (43.1% versus 16.5%), and ants threw away many more large larvae (74.6%) than in the wet season (28.2%). Many more small larvae were not removed from plants in the dry season (22.4%) than were large larvae (14.7%), but in the wet season, the reverse was true (61.8% large and 46.2% small were not removed).

Ant species also differed in how numbers and rates of larvae removed over the 2 h (Fig. 4; Table 3). On plants with *A. instabilis*, numbers of larvae per plant dropped significantly more quickly than on all other plants (Tukey's test, $P < 0.001$), and numbers dropped significantly more slowly on plants without ants than on all other plants ($P < 0.001$). Larval numbers fell at an intermediate pace on plants with *C. textor* and *Crematogaster* spp., but these two species did not differ ($P = 0.963$). Larvae removal rates significantly differed with ant species but this depended on larva size (Table 3). For small larvae, removal rates differed by species, but not with time interval. Removal rates were consistently higher on plants with *A. instabilis* than on plants with *C. textor* ($P < 0.001$) and with *Crematogaster* spp. ($P = 0.001$). Likewise, removal rates were higher on plants without ants than on plants with *C. textor* ($P = 0.019$). No other pairwise comparisons were significant. For large larvae, however, removal rates significantly differed with interval. Overall, removal rates were higher on plants with *A. instabilis* and than with *Crematogaster* spp. ($P = 0.04$) and rates on plants without ants were lower than all ant species ($P < 0.001$). However, differences were not consistent for all time intervals because of rapid drops in removal rates over the first intervals (Fig. 4).

Discussion

The three ant taxa studied here significantly differed in a number of ways related to their foraging activity and effects on experimentally introduced herbivores. The recruitment strategies of the ant species differed in both numbers of workers and recruitment rates, and two of the ant species used different recruitment strategies in the wet and dry seasons. Ants also had different effects on herbivores, and these effects varied somewhat with herbivore species and size but not with season. Ants affected herbivores in

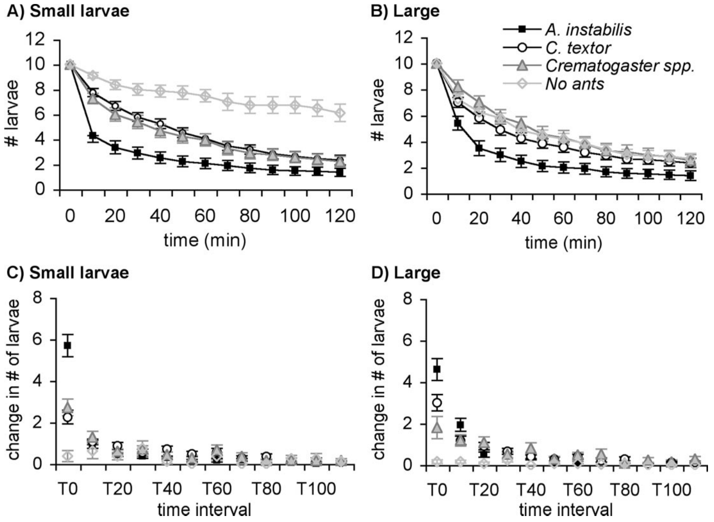

Fig. 4. Larvae removal on plants with three ant taxa or from which ants were removed with Tanglefoot. Graphs show average number of larvae remaining per plant every 10 min over a 2-h time period (A and B) and the removal rates (change in number of larvae between each 10-min interval) (C and D). Small larvae were ≈2–3 mm and large larvae were ≈5–8 mm. Error bars show SE.

different ways—the frequency with which ants either took away larvae differed from how often ants threw them off of coffee plants. At the low herbivore density, ants attacked one of two herbivore species more quickly. On plants where larvae were placed at high density, outcome frequencies differed with ant taxa and with herbivore size. Small larvae were removed much more often by *A. instabilis* and *C. textor*, but not by *Crematogaster* spp. Numbers and rates of herbivore removal over time differed with ant species, and this differed significantly with herbivore size. Finally, much higher proportions of herbivores were removed when introduced at low densities. The fact that so many differences in behaviors and effects of these three ant species were found especially given that the differences were not consistent for season, herbivore species, or herbivore size indicates that different ant species may have significantly different effects on prey communities as predators and that a diverse ant community may enhance the overall function of predation in coffee agroecosystems (Hooper et al. 2005). The fact that ants differed in their effects on small and large herbivores is an especially important result given that when predators use different resources (i.e., dif-

Table 3. Repeated-measures ANOVA examining for differences in no. of larvae removed and removal rate depending ant species (*A. instabilis*, *C. textor*, and *Crematogaster* spp., without ants) and season (wet and dry)

	df	MS	*F*	*P*
Number of larvae removed				
Ant species	3	2836.171	57.137	<0.001
Size	1	88.364	1.78	0.184
Ant species × size	3	75.544	1.522	0.210
Error (ant species)	204	49.638		
Time	11	255.027	281.319	<0.001
Time × ant species	33	11.683	12.887	<0.001
Time × size	11	1.165	1.286	0.279
Time × ant species × size	33	1.951	2.152	0.033
Error (time)	2,244	0.907		
Epsilon				0.227
Removal rate				
Ant species	3	8.377	20.403	<0.001
Size	1	0.3	0.730	0.394
Ant species × size	3	1.848	4.502	0.004
Error (ant species)	204	0.411		
Time	10	14.003	31.634	<0.001
Time × ant species	30	1.064	2.405	0.001
Time × size	10	0.361	0.817	0.561
Time × ant species × size	30	0.632	1.429	0.105
Error (time)	2,040	0.443		
Epsilon				0.625

P values were adjusted for lack of sphericity (Huynh-Feldt).

ferent sizes of herbivores), overall predatory effects may be enhanced and intraspecific competition reduced (Wilby et al. 2005). These observed differences set the backdrop for discussing the proposed mechanisms for how these behavioral differences may influence the function on these ants as predators.

Agroecologists have long touted that relatively high predator diversity (including both higher abundance and richness) in complex agroecosystems may generally better fulfill important pest regulation functions (Root 1973, Andow 1991, Provencher and Riechert 1994, Losey and Denno 1999). In a recent review, Hooper et al. (2005) summarized that predator diversity may be important to their function in one of two ways. First, having a large number of species increases the likelihood that one or more important predator species are included in the predator community. Second, presence of each predator species in a diverse group may increase function because of the diverse range of diets and foraging behaviors present. Some evidence suggests that a diverse group of predators combined at naturally observed densities may lower herbivore populations and increase plant yield more than when these predators are acting on their own (Cardinale et al. 2003). However, guaranteeing differences in predator behaviors and individual effects does not necessarily lead to enhanced function because of complex food web interactions. Interactions within the predator trophic level such as omnivory, intraguild predation, and ontogenetic or environmentally influenced diet shifts may strongly influence the ways in which predator effects combine in nature (Polis and Strong 1996). Thus, although behavior and function of predator species may differ, combinations of predators may result in entirely substitutable effects (Schmitz and Sokol-Hessner 2002, Sokol-Hessner and Schmitz 2002) or in nonlinear effects (Crumrine and Crowley 2003). Two recent studies have shown empirically that increased predator diversity may dampen trophic cascades and limit the effectiveness of predators in increasing plant biomass because of intraguild predation within the predator trophic level (Finke and Denno 2004, 2005).

Intraguild predation and interactions may be important when examining for effects between predator taxa, but not necessarily between these ant species because of their spatial organization. Here, we found that ants limited the amount of larvae removed by other predators. Many ants aggressively chase away pollinators (Altshuler 1999) and change foraging behaviors of important predators including birds (Aho et al. 1997, Haemig 1996), suggesting that ants may have negative effects on other predator groups. In coffee agroecosystems, *A. instabilis,* in high densities, limit foraging activity of insectivorous birds in canopy trees with potentially important implications for how the effects of this ant and birds may combine (Philpott et al. 2005). Thus, predator diversity, in the context of these three ant species in combination with other predator taxa, may not combine additively. However, on plants without ants, nearly one third of larvae were removed by other predators (lizards, wasps, birds) compared with only 1–5% on plants with the three ant species. This may reflect that other predators in coffee systems may compensate for changes in the predatory abilities of ants and lend support for the hypothesis that multiple predators positively influence predation. However, what are the effects of these three ant species combined? In tropical agroforests, dominant ants are spatially arranged in mosaic patterns whereby different species form mutually exclusive patches (Room 1975, Leston 1978). In the study site, *A. instabilis, C. textor,* and *Crematogaster* spp. form such patches in the coffee plants and also around particular shade trees (Philpott 2006). If ants are distinctly separate in time and space, and if the herbivores are highly mobile, the effects of the ants may be enhanced by maintaining each predator species more than if predator species actually occurred on the same plants, presumably because of lower interference between ant species. Most of the herbivore diversity is made up of lepidopteran larvae (we have recorded at least 30 different species feeding on coffee leaves in our study sites), which are relatively immobile as larvae. However, some herbivore species regarded as important pests by farmers in the region include relatively mobile species such as the coffee berry borer and a grasshopper (*Idiarthron subquadratum* Saussure and Pictet), which do damage to coffee as adults and nymphs, respectively (Segura et al. 2004). If these pests move frequently from patches with one ant species to patches with a different ant species, and if ant effects on these herbivores differ with time or season as observed here, or in the way they attack herbivores, ant diversity may be important in enhancing negative effects of ants on these pests. Finally, because these ant species do sometimes naturally occur both alone and in pairs, hypotheses regarding the combination of their effects could be tested experimentally in coffee agroecosystems.

A driving force in many of the interactions observed here, with particular importance to the coffee agroecosystem, was the overall efficiency of *A. instabilis* compared with the other species, but this may not be consistent under all conditions. Coffee was traditionally cultivated under a diverse, dense shade canopy, but recent production includes more intensive management—reducing vegetation complexity and diversity and using agrochemicals (Moguel and Toledo 1999). Coffee intensification results in losses of predator, specifically ant diversity (Philpott and Armbrecht 2006). Here, *A. instabilis* was the most effective predator. This species was the fastest recruiter and most quickly removed larvae at both high and low densities. In general, this species took away more larvae than it threw away, possibly leading to higher population level effects on herbivores. Interestingly, *A. instabilis* removed a much higher proportion of the herbivores introduced at high density than did the other species, perhaps reflecting a general foraging strategy covering entire plants, and not just restricted to certain areas. Perfecto and Vandermeer (2006) found this to be the case for *A. instabilis* preying on the coffee berry borer. They found that attack by the coffee berry borer was lower on plants with higher numbers of scale insects, yet this relationship was true on a per-plant, but not per-branch, level, indicating that scale presence increases ant activity on the entire plant, not just on particular branches. Thus, at first assessment, one conclusion may be that *A. instabilis* is the better predator. Coffee intensification limits the frequency with which *A. instabilis* occurs on coffee plants but does not affect *C. textor* or *Crematogaster* spp. (Philpott 2006). Thus, in addition to lowering ant diversity, intensification at the extreme end may eliminate this important predator species, lending evidence to support the hypothesis that as diversity is lost, we may by chance lose more important predators. However, the relative success of *A. instabilis* may not be consistent under all environmental conditions. *C. textor* and *Crematogaster* spp. removed just as many *E. acrea* larvae, and *C. textor* took away just as many small larvae when placed in high densities. Furthermore, because of unknown factors, *A. instabilis* occur in patches, and the effects of this predator on herbivores will therefore not be consistent across the landscape. This species, but not others, are also parasitized by a phorid fly (*Pseudacteon* sp.) and subsequently have limited effectiveness in preying on particular larvae when under attack (Philpott et al. 2004b). Importantly, where *A. instabilis* are attacked by phorids, other ant species including *C. textor* are significantly more likely to gain access to resources (Philpott 2005). Thus, where phorids actively limit *A. instabilis, C. textor* or other arboreal ant species may compensate for the limitation in *A. instabilis* in terms of predatory activity.

The observed differences in ant species may manifest themselves in enhanced function in coffee agroecosystems in several ways. There were differences in ant effects based on herbivore size, which may be an indication for differences in resource use, which could enhance predatory function. Because ant behavior and effects differed with season, different ant species may vary in response to changing environmental conditions. Specifically, because effects of ant species differed with changes in season, size, species, and density of herbivore, the variation in predatory roles of different ant species may provide better insurance in coffee agroecosystems when faced with drought, increased rain, new pest introductions, or other unpredictable changes (Yachi and Loreau 1999). Recruitment rates differed with season, and attack rates differed by herbivore species. It is likely that those ants recruiting to or attacking herbivores more quickly will have larger effects on limiting herbivory because herbivores have less time to feed before being discovered. Likewise, the differences in proportion of attacks where ants take versus throw larvae off plants might translate into differences in their effects on the prey base as those that are taken away are assumed effectively consumed by predators. Those that are thrown away may have a chance of getting back onto their host plants, if they are not first incorporated by other members of the predator assemblage on the ground. In the context of resource partitioning in particular, it will be critical to determine whether species differences, such as those observed here, are truly complimentary in trophic effects (Schmitz and Suttle 2001, Duffy 2002, Chalcraft and Resetarits 2003, Wilby et al. 2005). In behavioral observations of three co-occurring predators, Montserrat et al. (2004) found that two species that remained near high pest densities had consistently high consumption rates but were nonetheless complemented by a third predator that did not consume much prey but stayed on plants with low pest populations. The authors hypothesized that the behavioral differences of these predators act synergistically especially in habitats with spatial variation in prey populations. From our data, we cannot determine whether ant species are complimentary, but their behavioral diversity lends itself toward future work in this area.

This study makes some interesting observations relating to behavioral differences of a few common ant species in coffee agroecosystems; they differ in foraging strategies and in their effects on herbivores, and to some extent, the ways in which ants respond to herbivores differs with season, size, and species of larva. It is possible that these behavioral differences between these three ant species may increase their functional diversity in coffee agroecosystems. There are obvious shortcomings of this observational approach—from these data, we cannot assess if the effects of these ant species are additive or compensatory, and thus cannot judge whether their effects in the coffee food web are complimentary. Nor can we assess how the effects of these ants on lower trophic levels might change in response to drastic changes in environmental conditions. However, this study does inform us as to whether predator species common in the coffee agroecosystem environment differ in behaviors and their effects on herbivores, indicating that that arboreal ant species do differ and may be functionally diverse predators.

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