APHIDS ALTER THE COMMUNITY-WIDE IMPACT OF FIRE ANTS

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Abstract. Positive species interactions have the potential to strongly influence the structure and dynamics of ecological communities, yet surprisingly few studies have documented their general importance. We tested the hypothesis that the mutualistic association between fire ants and aphids enhances the impact of fire ants on the herbivorous and predaceous arthropod community of cotton. We found that the presence of aphids attracted foraging fire ants onto cotton plants. This shift from ground to foliar foraging resulted in more frequent interactions between fire ants and arthropods associated with cotton. The survival of herbivores (caterpillars) and predators (ladybird beetles and lacewings) was lower in the presence of fire ants and aphids compared with fire ants alone in greenhouse experiments. Similarly, fire ants and aphids deterred plant bugs from spending time on cotton foliage. Using large-scale field manipulations of fire ants along with naturally occurring aphid populations, we found that the ant–aphid mutualism accounted for much of the variation underlying ant impact on cotton herbivores and predators. For example, in 2001, ~27% of herbivore taxa and 54% of predator taxa were adversely affected by the mutualism. The overall community response, however, was highly conditional with strong temporal variation in the effects of the ant–aphid association. Our results indicate that the relationship between fire ants and aphids serves as a key interaction that alters the structure of cotton arthropod communities. This conclusion has far-reaching significance for understanding food web dynamics in natural systems and the efficacy of biological control in ant-infested areas.

Key words: agroecology; ant–homopteran mutualism; arthropod community dynamics; Aphis gossypii; *biological control; cotton aphid; indirect effects; invasive ant; keystone mutualism; predator–prey interaction; red imported fire ant;* Solenopsis invicta.

INTRODUCTION

Population and community ecology have historically focused on the importance of negative species interactions, such as predation and competition, as factors regulating the distribution and abundance of animals and plants (Bronstein 1994*b*, Stachowicz 2001). Yet a growing number of studies espouse the central role of positive interactions (e.g., facilitation and mutualism) in shaping the structure and dynamics of diverse ecological communities (Boucher et al. 1982, Bronstein 1994*b*, Stachowicz 2001, Bruno et al. 2003). The relationships between pollinators, seed dispersers, and flowering plants have long been touted as fundamental examples of mutualism (Boucher et al. 1982, Bronstein 1994*b*). However, more recent studies reveal positive associations among organisms traditionally considered as antagonists. For instance, herbivores are typically thought to compete for limited resources, yet they may also facilitate one another by creating habitat as demonstrated by the engineering effects of shelter-building

caterpillars (Martinsen et al. 2000, Lill and Marquis 2003).

One of the most widely recognized and well-cited examples of mutualism can be found in the relationship between ants and honeydew-producing hemipterans (e.g., aphids and scale insects). Ants are attracted to honeydew, a sugar-rich solution excreted by many hemipterans, and subsequently ''tend'' the hemipterans, providing protection from their natural enemies (Way 1963). In a similar manner, ants may also attack phytophagous competitors of hemipterans that feed on the same host plant (Nickerson et al. 1977, Messina 1981, Ito and Higashi 1991, Floate and Whitham 1994). In fact, many ants display ownership behavior while tending hemipterans and attack insects that they might otherwise tolerate (Way 1963). Furthermore, hemipterans may attract ants onto the foliage of plants, increasing the likelihood that ants will encounter other arthropods and thus have a greater impact on plant-based food webs. As a result, honeydew-producing insects have the potential for generating strong indirect effects on arthropod communities by manipulating the behavior and abundance of ants foraging on plants. Unfortunately, previous studies have overwhelmingly focused on one species or guild of insect and thus research aimed at quantifying the community-wide effects of ant–hemipteran mutualisms is typically not considered

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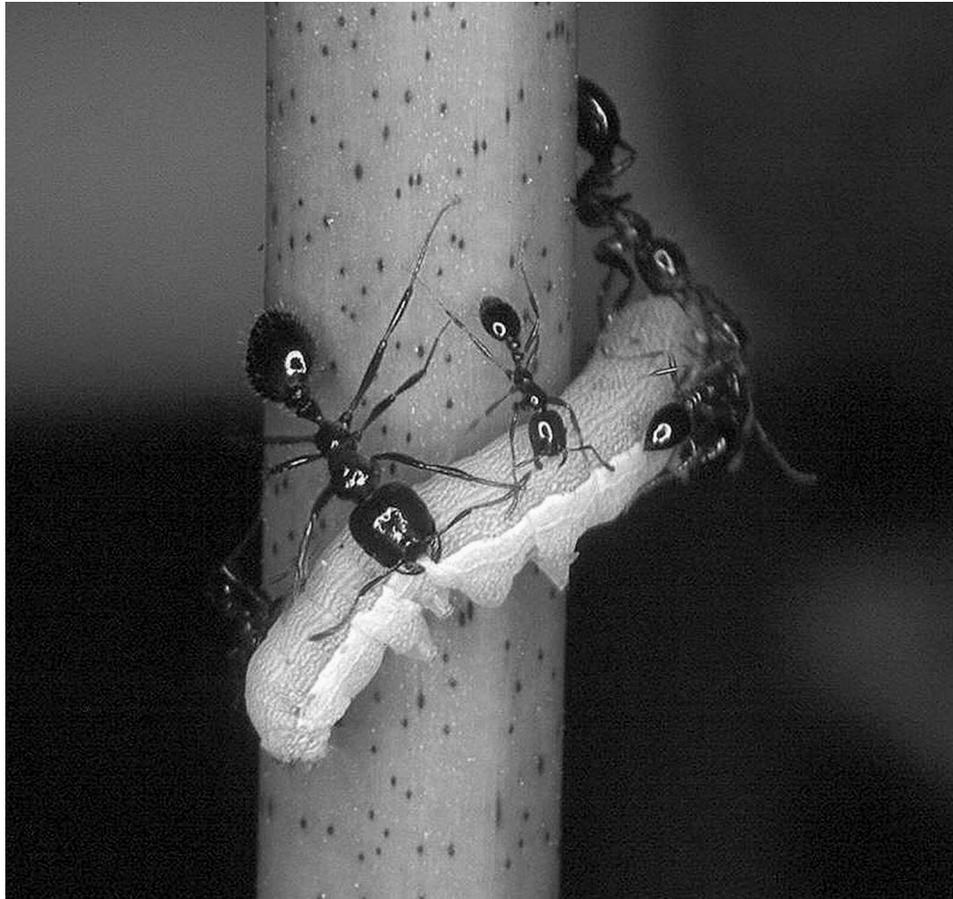
PLATE. 1. Red imported fire ants transporting a paralyzed beet armyworm caterpillar down the stem of a cotton plant to their colony. Photo credit: Takumasa Kondo. A color version of this photograph is available in Appendix B.

(but see Wimp and Whitham 2001). Studies based on ant–plant mutualisms suggest that extrafloral nectar (a sugary, plant-derived secretion similar in composition to honeydew) can mediate complex tri-trophic relationships, and therefore a similar role for hemipteran honeydew is certainly plausible (Rudgers and Gardener 2004).

We studied the interaction between cotton aphids, *Aphis gossypii* (Hemiptera: Aphididae), and red imported fire ants, *Solenopsis invicta* (Hymenoptera: Formicidae; see Plate 1), a dominant predator throughout the southern United States. Fire ants have invaded many ecosystems and have gained notoriety for their pervasive effects in non-native habitats (Vinson 1997, Holway et al. 2002). In particular, agricultural food webs appear to be especially prone to strong multitrophic interactions involving fire ants and other insects (Risch and Carroll 1982, Way and Khoo 1992, Eubanks 2001, Eubanks et al. 2002). However, our previous research in agriculture-based arthropod communities suggested extensive variation in the impact of fire ants. We manipulated fire ant abundances in several crops and recorded relatively weak effects of fire ants on

arthropods in soybean and collards, but a comparatively strong impact of fire ants in cotton (Eubanks 2001, Eubanks et al. 2002, Harvey and Eubanks 2004; M. Eubanks, *unpublished data*). One of the main differences between these systems is that cotton is a host plant for an abundant, honeydew-producing insect (the cotton aphid), whereas soybean and collards are not. Because earlier studies have documented that fire ants readily tend cotton aphids (Kaplan and Eubanks 2002), we suggest that the differences in responses among systems may derive from the mutualism found between fire ants and aphids in cotton. The cotton system provides an ideal assemblage of arthropods for testing hypotheses on the community-wide impact of ant–aphid interactions. Cotton fields sustain many arthropod species and the resulting food web is likely to be highly reticulate because of the rich fauna of omnivorous arthropods, the relatively large number of intermediate predators that frequently serve as intraguild prey, and the presence of many higher-order enemies that are known to be significant intraguild predators (Rosenheim et al. 1993, Knutson and Ruberson 1996, Eubanks 2001, Eubanks et al. 2002).

We hypothesized that fire ants would more strongly suppress the densities of cotton arthropods when found in association with aphids. Thus, our main predictions are that aphids attract fire ants, causing them to forage more frequently on cotton plants, and, as a result, fire ants have a greater impact on herbivores and predators in the presence of aphids than in their absence. This study highlights the central role that positive species interactions such as mutualisms may play in mediating community-level interactions and thus dictating trophic structure.

METHODS

Numerical response of fire ants to aphids

We determined whether ants alter their foraging behavior (i.e., increase foliar foraging) in the presence of aphids using a greenhouse experiment. Cotton was grown from seed in the greenhouse and plants were selected for experiments when they contained 5–6 true leaves (~1 m tall); we used different potted plants for each experimental replicate. Plants were placed individually in cages with potting soil and field-collected colonies of fire ants (~500 ants per cage) were given access to cages using foraging tunnels (see Kaplan and Eubanks 2002 for details of cage design). We randomly assigned one of four treatments to caged plants: no aphids, low aphid density (~10 aphids/leaf), medium aphid density (~25 aphids/leaf), and high aphid density (~50 aphids/leaf). These densities correspond with those commonly encountered within local cotton fields during the course of a field season (M. Eubanks, *unpublished data*). Aphids were selected from a greenhouse colony and allowed to acclimate on experimental plants for 24 h. Fire ants were then given access to cages and, after 24 h, we counted the number of ants foraging on plants. Each treatment combination was replicated 20 times over three different dates and ant densities were compared between aphid treatments using analysis of variance with date as a blocking factor (all statistical analyses used SAS, version 8.2; SAS Institute 1995).

We collected corresponding data to document the relationship between cotton aphid and fire ant densities on cotton plants in the field. In 2002, cotton plants were randomly sampled in a 5-ha field that was not used for experiments. We performed a combination of beat cloth and visual samples on randomly chosen plants. Beat cloth samples were performed by vigorously shaking one cotton plant over a 1-m² cloth; all dislodged ants were counted and recorded. Visual sampling was subsequently performed on the same plant, which consisted of searching the upper six leaves of a cotton plant, counting all visible aphids on the top and bottom of each leaf. Because aphids mainly occupied cotton fields early in the season, we sampled during the aphid peak, 14 June through 12 July (9–12 samples/week; 49 total beat cloth and visual samples). The re-

lationship between log-transformed densities of cotton aphids and fire ants was examined using Pearson's product-moment correlation.

Effect of ant–aphid mutualism on herbivores/predators: greenhouse experiments

We performed a series of greenhouse experiments designed to quantify the indirect effect of aphids on cotton arthropods mediated through their interaction with fire ants. Three treatments were randomly assigned to caged cotton plants (same general cage design as described in the above section): no aphids, low aphid density (~10 aphids/leaf), and high aphid density (~50 aphids/leaf). Fire ants were allowed access to all caged cotton plants for 24 h to begin tending aphids. As a result, there were no ant-free treatments that tested for the direct effects of aphids on cotton herbivores. However, we found no indication of negative interactions between aphids and other herbivores in the absence of fire ants (M. Eubanks, *unpublished data*). The densities of all insects used in greenhouse experiments are within the natural ranges encountered in Alabama cotton fields (Eubanks 2001).

In our first experiment, seven third-instar beet armyworm larvae, *Spodoptera exigua* (Lepidoptera: Noctuidae), were placed on the foliage of caged plants in all three treatments. *Spodoptera exigua* is a common, foliage-feeding herbivore that is often regarded as a serious pest by cotton growers (Mascarenhas et al. 1999). Caterpillar eggs were obtained from a colony located at North Carolina State University (Raleigh, North Carolina, USA) and reared to the third instar in a growth chamber at Auburn University (Auburn, Alabama, USA). We recorded *S. exigua* survival over a 6 h time period (at 0.5, 1, 1.5, 2, 3, 4, and 6 h) by repeatedly counting caterpillars remaining on cotton plants. Each treatment combination was replicated 12 times (four replicates on three separate dates). The proportion of surviving caterpillars was arcsine square-root transformed and caterpillar survival was analyzed using a repeated-measures ANOVA with date as a blocking factor (SAS ProcMixed; Khattree and Naik 1999).

In a second experiment, one adult tarnished plant bug, *Lygus lineolaris* (Hemiptera: Miridae), was placed on each cotton plant in all three aphid-density treatments. Similar to armyworms, *L. lineolaris* are extremely common herbivores that have emerged as a primary cotton pest (Hanny et al. 1977). Plant bugs were collected in local cotton fields and adjacent uncultivated vegetation and kept individually in vials stored in a growth chamber at 14°C for approximately 24 h before use in experiments. The survival of *L. lineolaris* was recorded over a 6-h time period in experimental cages. The number of surviving plant bugs was compared between treatments using a 3 × 2 contingency table (Sokal and Rohlf 1995). We also observed plant bugs for 1 min per cage (four total ob-

servations per cage) and noted their location and be-havior. Each treatment combination was replicated 17 times (five replicates on one date and six replicates on two other dates). The number of seconds per minute that *L. lineolaris* spent on plant foliage or stems was analyzed using a repeated-measures ANOVA, blocked by date.

In the third and fourth experiments, either two la-dybird beetle larvae, *Coccinella septempunctata* or *Hippodamia convergens* (Coleoptera: Coccinellidae), or two lacewing larvae, *Chrysoperla carnea* (Neurop-tera: Chrysopidae), were placed on the foliage of caged plants with either aphids present (~25 aphids/leaf) or aphids absent; fire ants were present in all cages. Lady-bird beetles and lacewings are commonly encoun-tered natural enemies in cotton fields and are consid-ered beneficial for the control of herbivores. Ladybird beetles were collected from local cotton fields and kept individually in vials for 24 h prior to use in experi-ments. Ladybird beetles were randomly selected to mimic the mix of *C. septempunctata* and *H. convergens* found naturally in cotton fields. Lacewings were ob-tained from a commercial supplier (Beneficial Insec-tary, Redding, CA, USA). Fire ants were given access to all caged plants and we compared the number of larvae remaining after 24 h in the presence and absence of aphids using a 2 × 2 contingency table (Sokal and Rohlf 1995). Treatment combinations were replicated 15 times for the ladybird beetle experiment and 10 times for the lacewing experiment.

Effect of ant–aphid mutualism on herbivores/ predators: field experiment

The field experiment was designed to measure the relationship between aphids and other cotton arthro-pods in plots where fire ants were present vs. plots where fire ants were experimentally excluded. Research was conducted over the course of two field seasons at the E.V. Smith Agricultural Experiment Station (Tal-lassee, Alabama, USA). During the 2001 season, we used two large fields (~12 ha each) that each encom-passed six 1.2-ha plots and one smaller field (~4 ha) that was divided into two 1.2-ha plots (14 total plots). All fields were separated by 1–2 km. In 2002, we used one large field (~10 ha) subdivided into twelve 0.4-ha plots. All plots during both years were separated by a >50 m boundary of cotton that was not used for sam-pling. Plots were randomly assigned to ant-density treatments (high or low) and we manipulated ant abun-dance with Amdro (American Cyanamid, Wayne, New Jersey, USA), a commercially available fire ant bait. Amdro is a granular insecticide that is very effective at suppressing fire ant densities with little or no impact on nontarget arthropods (see Eubanks et al. 2002, Kap-lan and Eubanks 2002). This bait is composed of an inert, corn ''grit'' carrier impregnated with soybean oil that is very attractive to foraging fire ants but ignored by other insects. Hydramethylnon, the insecticide, is

incorporated into the oil. Foraging ants find the bait and carry it back to their colony where the toxicant is spread throughout the mound, and all members of the colony are affected. In treated plots (low fire ant den-sity), Amdro was applied 2–4 times during the season at a rate of 1 kg/acre. Control plots (high fire ant den-sity) were naturally colonized by fire ants.

Cotton arthropods were sampled approximately weekly between June and August during the 2001 and 2002 field seasons (see Appendix A for a list of all arthropods sampled). In 2001, six samples were taken per plot and in 2002, three samples were taken per plot. Arthropod sampling was performed through a combi-nation of beat cloth and visual samples. A 1-m^2 cloth was placed on the ground between two rows of cotton at a random location within the plot. Beat cloth samples were performed by vigorously shaking six cotton plants (three from each row) over the cloth. All dislodged arthropods were quickly identified, counted, and re-corded. Visual sampling was subsequently performed on one of these six cotton plants to obtain an estimate of aphid density at that location within the plot. Ar-thropod densities (per visual/beat cloth sample) were $\log(n + 1)$ transformed to meet assumptions of nor-mality. Fire ant densities were compared between Amdro-treated and control plots using a repeated-mea-sures ANOVA. The densities of herbivorous and pre-daceous arthropods were compared using a repeated-measures heterogeneity of slopes model, with high and low fire ant densities as main effects and aphid density as a covariate. Field data met all assumptions required for use of the repeated-measures analysis. In 2001, field was used as a blocking factor. The full model was tested hierarchically beginning with the highest order (three-way) interaction between date, ant, and aphid. Nonsig-nificant three-way interactions were pooled into the error before testing the next effect in the hierarchy (in this case, ant × aphid or date × ant) (Sokal and Rohlf 1995). A Bonferroni correction was used to account for inflation of type I error associated with performing multiple significance tests (2001, significance level = 0.05/32 taxa = 0.0016; 2002, significance level = 0.05/ 29 taxa = 0.0017). However, this provides a highly conservative estimate of ant–aphid effects on the ar-thropod community and as a result this analysis may fail to detect biologically important interactions (Mor-an 2003). Therefore, both Bonferroni-corrected and un-corrected analyses are presented. For those taxa with significant two- or three-way interaction terms, the tests for main effects may be spurious and should be inter-preted with caution. However, the primary intention of these analyses was to detect significant interactions in-volving ants and aphids, therefore main effects were of secondary importance.

A significant statistical interaction involving the ant treatment and the aphid covariate indicates that a dif-ferent relationship exists between aphids and arthro-pods in the presence of ants than in their absence.
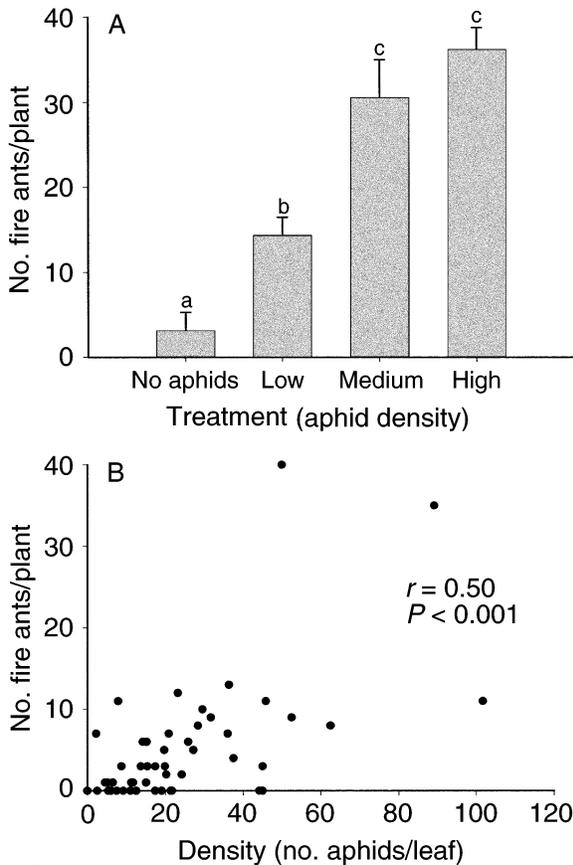
FIG. 1. The relationship between fire ant recruitment onto cotton plants and aphid density in (A) a greenhouse experiment (means + SE) and (B) field sampling. In panel A, different letters indicate means that are different at the $P = 0.05$ level (Bonferroni test).

Therefore, significant interaction terms involving ants and aphids were used to quantify the community response to this mutualism. All taxa were subdivided into categories based on their trophic level (predator vs. herbivore), diet breadth (generalist vs. specialist), mobility (mobile vs. sedentary), size (large vs. small), and numerical dominance (Appendix A). Predators that primarily feed on aphids, including ladybird beetles and lacewings, were referred to as aphid specialists. All other enemies in the community consume aphids to varying degrees, but have more diverse diets and thus were designated as generalist predators (see Knutson and Ruberson 1996). The diet breadth of herbivores was not assessed since this information provides no insight to the potential relationship between these insects and aphids or fire ants. The presence or absence of wings was used to assess mobility. Arthropods possessing functional wings were referred to as mobile, while nonwinged taxa or life stages were called sedentary. All taxa in which adults (winged) were undifferentiated from immature (nonwinged) stages were excluded from the analysis (e.g., Cicadellidae, *Neuro-*

colpus nubilus, Orthoptera, Anthocoridae, Reduviidae). The arthropod community was separated into large and small species based on body size. An arbitrary cutoff of 5 mm or less was used to designate small species, while arthropods >5 mm were classified as large. The life stages of certain species varied greatly in size (e.g., lepidopteran, lacewing, and ladybird beetle larvae) and therefore these insects were not assigned to either category. Dominance was measured by assessing the abundance of each taxon averaged over the 2001 and 2002 field seasons and expressed as a percentage of the overall herbivore or predator communities. Within year comparisons between factors were made using the chi-square test (SAS ProcFreq).

RESULTS

Numerical response of fire ants to aphids

More ants were found foraging on cotton plants that hosted aphids than on aphid-free plants in our greenhouse experiment (Fig. 1A; $F = 40.53$, df = 3, $P < 0.0001$). In addition, we found a positive correlation between fire ant and cotton aphid densities on plants in the field (Fig. 1B; $r = 0.50$, $P < 0.001$).

Effect of ant–aphid mutualism on herbivores/ predators: greenhouse experiments

Fewer caterpillars survived on plants with fire ants and aphids than on plants with fire ants alone (Fig. 2A; $F_{2, 236} = 40.87$, $P < 0.0001$); this effect was intensified with increasing aphid density. On high-aphid-density plants, ants were frequently observed attacking and consuming caterpillars (see Plate 1 and Appendix B).

In a similar greenhouse experiment, aphids did not affect tarnished plant bug survival in the presence of fire ants ($G = 0.38$, df = 2, $P > 0.05$). Fire ants did, however, discourage tarnished plant bugs from spending time, and subsequently feeding, on cotton plants (Fig. 2B; $F_{2,44} = 3.22$, $P < 0.05$).

Predator survival was lower in the presence of fire ants on aphid-infested plants vs. aphid-free plants in the greenhouse (Fig. 2C). Ladybird beetle survival was reduced by 84% ($G = 6.52$, df = 1, $P < 0.025$) and lacewing survival was reduced by 76% ($G = 4.08$, df = 1, $P < 0.05$) in the presence of aphids and fire ants compared with fire ants alone.

Effect of ant–aphid mutualism on herbivores/ predators: field experiment

In 2001, fire ants were more than twice as abundant in control plots (2.89 ± 0.31 fire ants/sample) than in Amdro-treated plots (1.37 ± 0.16 fire ants/sample) (Fig. 3A; $F_{1,10} = 7.59$, $P < 0.05$). In 2002, fire ants were >10× as abundant in control plots (5.39 ± 0.55 fire ants/sample) than in Amdro-treated plots (0.50 ± 0.10 fire ants/sample) (Fig. 3B; $F_{1,70} = 126.75$, $P < 0.0001$).

During the 2001 and 2002 field seasons, the interaction between fire ants and aphids frequently account-
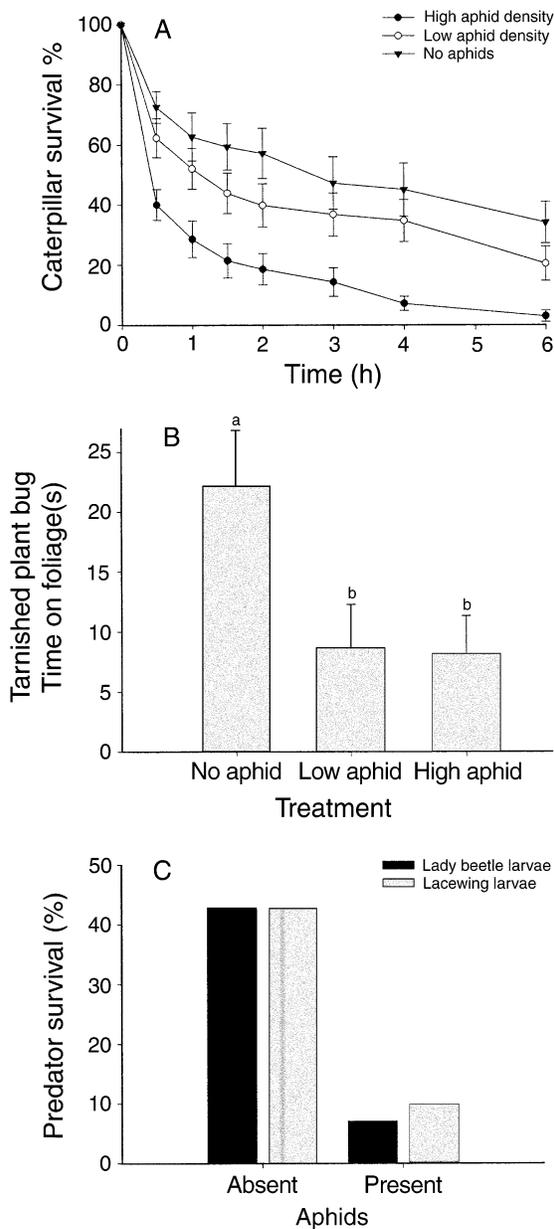
FIG. 2. The effect of aphids, in the presence of fire ants, on (A) caterpillar survival, (B) tarnished plant bug behavior, and (C) predator survival in greenhouse cage experiments. Means ($\pm$SE) with different letters are different at the $P = 0.05$ level (Bonferroni test).

ed for significant variation in the abundances of cotton herbivores and predators (Appendices C and D, ant $\times$ aphid or date $\times$ ant $\times$ aphid effect). In 2001, three of 11 herbivores and nine of 19 predators were significantly affected by the ant–aphid mutualism; one herbivore and three predators remained significant after Bonferroni correction (Appendix C). In 2002, four of 12 herbivores and six of 15 predators (as well as total predators) were significantly affected by the ant–aphid mutualism; two herbivores, three predators, and total

predators remained significant after Bonferroni correction (Appendix D). In the majority of cases the three-way interaction between date, ant, and aphid was significant, indicating that the interactive effects of fire ants and aphids varied greatly from week to week. For instance, the relationship between aphids and many cotton arthropods differed between high and low-fire-ant density plots depending on sampling date (Appendix E).

Four factors (trophic level, diet breadth, dispersal ability, and body size) were used to assess the community response to the ant–aphid mutualism (Table 1). No significant differences were found in the percentage of taxa responding to ant–aphid interactions for comparisons between predators vs. herbivores (2001, $\chi^2 = 1.73$, $P = 0.19$; 2002, $\chi^2 = 0.13$, $P = 0.72$), specialists vs. generalists (2001, $\chi^2 = 0.03$, $P = 0.85$; 2002, $\chi^2 = 0.07$, $P = 0.79$), or mobile vs. sedentary arthropods (2001, $\chi^2 = 1.00$, $P = 0.32$; 2002, $\chi^2 = 0.01$, $P = 0.94$). In 2002 we detected a significant difference between large and small arthropods ($\chi^2 = 5.49$, $P = 0.02$), but not in 2001 ($\chi^2 = 0.04$, $P = 0.84$).
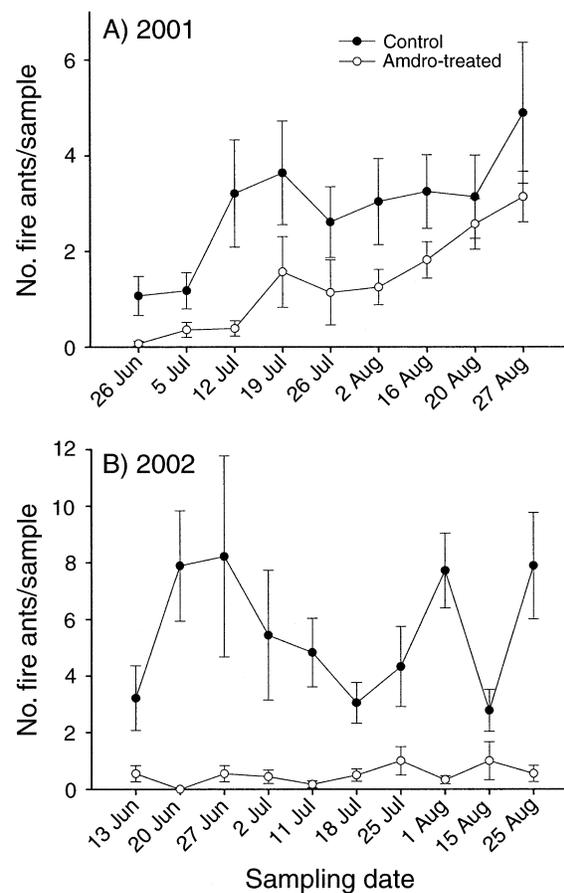

FIG. 3. The densities of fire ants (mean $\pm$ SE) in control (high fire ant) and Amdro-treated (low fire ant) field plots during the (A) 2001 and (B) 2002 seasons.

TABLE 1. Factors influencing the arthropod community response to ant–aphid interactions during the 2001 and 2002 field seasons.

	2001		2002	
Factor	(%)	*n*	(%)	*n*
Trophic level				
Predator	54	13	40	15
Herbivore	27	11	33	12
Diet breadth				
Aphid specialist	50	4	33	3
Generalist predator	55	9	42	12
Dispersal ability				
Mobile	37	8	40	10
Sedentary	62	8	42	12
Body size				
Large (>5 mm)	40	10	18	11
Small (<5 mm)	44	9	67	12

Notes: Percentages reflect the fraction of the overall community (percentage of taxa/life stages) that responded with significant two- or three-way interactions involving fire ants and aphids (see Appendices C and D). Sample size *n* is the number of arthropod taxa/life stages examined for that particular factor, level, and year.

DISCUSSION

Our research provides data from two years of large-scale manipulative field experiments combined with detailed greenhouse studies which, together, suggest that aphids alter the impact of fire ants on a diverse assemblage of arthropods. Yet, compared with greenhouse results in which aphids consistently enhanced ant effects, field results indicate that under natural conditions, aphids have the potential to enhance the impact of fire ants, but not in all circumstances. The interactive effects of ants and aphids were not equally strong across the entire cotton community or on all sampling dates. These two major forms of variation are now discussed to characterize both the community response to ant–aphid interactions and the conditionality of this mutualism (temporal variation).

Community response to ant–aphid mutualism

The overall community response to ant–aphid interactions was by no means uniformly distributed across taxa. Rather, certain factors appeared to predispose some members of the community to respond more strongly than others (Table 1). For instance, there was a consistent, albeit nonsignificant, trend for predators to suffer adverse consequences from ant–aphid effects compared with herbivores (2001, 54% predators vs. 27% herbivores; 2002, 40% predators vs. 33% herbivores). This outcome is not surprising given the spatial proximity of fire ants and predators foraging in the canopy of plants. Both ants and predators are strongly attracted to aphids (albeit for different reasons, ants collecting honeydew while predators consuming aphids) and thus are likely to aggregate and more frequently encounter one another on plants with high aphid densities. Also, ants have only negative effects on predator populations, whereas ants may have both direct negative (through consumption) and indirect positive effects (by reducing the densities of other enemies via intraguild predation) on herbivores (Eubanks 2001). Because fire ants are known to be major intraguild predators in the cotton community herbivores may indirectly benefit by experiencing reduced top-down pressure from key predators and parasitoids (Rosenheim et al. 1993, Eubanks et al. 2002).

There was no significant difference in the response of generalist predators to ant–aphid effects compared with aphid specialists, although generalists were slightly more likely to be affected than specialists (2001, 50% specialists vs. 55% generalists; 2002, 33% specialists vs. 42% generalists). This finding was unexpected and contrary to the prediction that fire ants should more strongly interact with aphid specialists than generalist predators. Knutson and Ruberson (1996) concluded that fire ants "probably have little impact on populations of predatory insects or spiders in cotton, except those feeding on aphids." The enemies sampled in our study, however, were dominated by a diverse guild of generalist predators, most of which readily consume cotton aphids (Knutson and Ruberson 1996). Thus, a large proportion of the total enemy community consisted of aphid feeders. Furthermore, aphids were the most abundant herbivore (both numerically and in terms of overall biomass) in the cotton community during the two years of this study (M. Eubanks, *unpublished data*). As a result, we suspect that aphids represent a primary prey item for opportunistic consumers in this system and that many generalist predators may behave similar to specialists due to the inordinately high representation of aphids in their diet.

The remaining two factors examined were mobility and body size. In 2001, there was a trend for relatively sedentary arthropods to respond more strongly than highly mobile taxa, although this trend disappeared the following year (2001, 37 vs. 62%; 2002, 40 vs. 42%; mobile vs. sedentary). As demonstrated by greenhouse experiments (Fig. 2), the densities of nonwinged arthropods (e.g., caterpillars and larval predators) are reduced through consumption by foraging ants (density-mediated effects), whereas mobile species (e.g., tarnished plant bugs) are influenced through nontrophic, behavioral responses to ant attack (trait-mediated effects) (see Rudgers et al. 2003). Thus, despite the fact that sedentary taxa were more frequently consumed by ants, it may be difficult to detect an effect of dispersal ability on arthropod abundance in the field since mobile prey often emigrate in response to predation risk (Cronin et al. 2004). In spite of the potential drawbacks associated with low mobility, our data suggest that attaining a large body size provides partial refuge from foraging ants. In 2002, small arthropods were significantly more likely to be affected than large taxa (2001,

40% large vs. 44% small; 2002, 18% large vs. 67% small). We found this rather surprising since ants are renowned for their ability to subdue large prey items, particularly aggressive species such as fire ants (Höll-dobler and Wilson 1990). However, we hypothesize that the advantage of being large is not a consequence of providing better resistance to attack, but rather it offers greater mobility in evading harassment by pugnacious ants. For instance, large spiders such as the green lynx, *Peucetia viridans*, are extremely agile and swiftly jump between branches when threatened by potential enemies (see Eubanks et al. 2002).

Temporal variation in ant–aphid mutualism

Mutualisms (and other types of species interactions) were traditionally thought to function with relative constancy across space and time. Yet recent reviews have emphasized the conditionality of mutualistic interactions (Bronstein 1994*a*, Bronstein and Barbosa 2002). Under certain biotic and environmental conditions, two species may behave as mutualists, while under alternative circumstances the nature of the interaction can change drastically (e.g., van Ommeren and Whitham 2002). We suspect that the association between fire ants and cotton aphids similarly varies both within and among field seasons (compare number of significant three-way interactions involving date vs. two-way ant–aphid interactions; Appendices C and D). The interactive effects of ants and aphids were not consistently strong across all sampling dates, but rather the intensity of their interaction fluctuated greatly from week to week (Appendix E). Such fluctuations are not altogether surprising given the range of potential factors known to vary with time. Primarily, ant and aphid densities do not remain constant, which undoubtedly influences the outcome of their interaction. Ant densities generally increase throughout the summer months resulting in highest densities late in the season (Fig. 3). Aphid populations fluctuate dramatically with a large early-season outbreak, followed by a severe mid-season crash and a small late-season peak (Kaplan and Eubanks 2002). As a result, temporal changes in the nature of the ant–aphid mutualism are to be expected. For instance, certain ant species will begin consuming aphids as a source of protein when aphid populations reach very high densities and thus ants may no longer protect these aggregations (Way 1963). Similarly, when ant or aphid densities reach an upper or lower threshold this will likely influence the number of ants tending aphids (and consequently foraging on plants) or how aggressively they defend this resource. Other aspects of the mutualism may have also changed with time, including the dietary preference of fire ant colonies (e.g., carbohydrate vs. protein; Stein et al. 1990) and the quality or quantity of honeydew produced by aphids (Henneberry et al. 2000). Unfortunately we were unable to detect similarity in the temporal sequence of ant–aphid effects among arthropod taxa, nor could we link variation in the direction of ant–aphid effects with peaks in ant/aphid abundances. As a result, the factor(s) driving these strong temporal fluctuations remains unclear.

Implications of ant–aphid mutualism for biological control

The potential for hemipterans to act as positive contributors to biological control by enhancing the performance of natural enemies has previously been recognized (Way and Khoo 1992, Lach 2003), although few studies have experimentally tested this concept. In our study system, the negative, indirect effects of cotton aphids on arthropods create contradictory potential outcomes for the biological control of herbivores. In one respect, aphids could indirectly reduce herbivore densities in cotton fields by increasing the frequency of interactions between ants and herbivores (e.g., Messina 1981). An alternative scenario may arise if aphids interfere with biological control through encouraging intraguild interactions between fire ants and other, potentially more effective, natural enemies (e.g., Fritz 1983). Intraguild predation by fire ants, however, does not appear to interfere with biocontrol in this system (M. Eubanks, *unpublished data*). Fire ants are voracious predators that attack a wide variety of herbivores and are numerically dominant in Alabama cotton fields (Eubanks 2001). Thus a reduction in the abundance of other cotton predators by fire ants may not strongly affect biocontrol since fire ants are such dominant consumers.

An additional consideration is the pest status of aphids relative to other herbivores, since aphid densities are considerably higher when tended by fire ants (Kaplan and Eubanks 2002). When aphids feed in large aggregations and other herbivores (e.g., caterpillars, plant bugs) are at low densities, the mutualistic ant–aphid relationship will likely be detrimental for cotton growth and yield since aphids are damaging plants while providing no beneficial services. When both aphids and other herbivores are at outbreak densities, however, the ant–aphid association may benefit cotton plants by enhancing predation on other, potentially more damaging, herbivores (see "byproduct mutualism" of Lach 2003). For example, Ito and Higashi (1991) found that the presence of *Formica* ants on oak trees resulted in a ~300% increase in aphid densities, yet ants also protected acorns from lepidopteran borers and as a result doubled the output of viable seeds. Since cotton aphids only cause yield loss at extremely high densities (Rosenheim et al. 1997), we suspect that these aphids similarly benefit cotton plants by attracting beneficial hymenopterans such as fire ants, although the overall impact of the mutualism on cotton fitness remains unknown (J. Styrsky and M. Eubanks, *unpublished data*).

Conclusions

Our results are consistent with previous reports of honeydew-producing hemipterans that act as facilitators of predaceous ants (Nickerson et al. 1977, Messina 1981, Ito and Higashi 1991, Floate and Whitham 1994, Wimp and Whitham 2001). However, unlike most prior studies, which focus on one or a few key taxa of interest, our study demonstrates a pervasive community-wide effect of this mutualism. Importantly, fire ants are a key invasive species in the southern United States, and thus understanding the consequences of their relationship with mutualistic hemipterans may provide greater mechanistic insight to their detrimental effects on native animal communities and potentially beneficial impact as top predators in agricultural food webs.

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APPENDIX A

A table showing arthropod taxa sampled during the field experiment and their diet breadth, mobility, size, and dominance is available in ESA's Electronic Data Archive: *Ecological Archives* E086-089-A1.

APPENDIX B

A color version of the Plate 1 photograph (taken by Takumasa Kondo) of red imported fire ants transporting a paralyzed beet armyworm caterpillar down the stem of a cotton plant to their colony is available in ESA's Electronic Data Archive: *Ecological Archives* E086-089-A2.

APPENDIX C

Results of repeated-measures analysis of variance for the effects of field, date, fire ants, aphids, date × fire ants, fire ants × aphids, and date × fire ants × aphids on the community of cotton arthropods during the 2001 field season are available in ESA's Electronic Data Archive: *Ecological Archives* E086-089-A3.

APPENDIX D

Results of repeated-measures analysis of variance for the effects of field, date, fire ants, aphids, date × fire ants, fire ants × aphids, and date × fire ants × aphids on the community of cotton arthropods during the 2002 field season are available in ESA's Electronic Data Archive: *Ecological Archives* E086-089-A4.

APPENDIX E

A figure showing temporal variation in ant–aphid effects is available in ESA's Electronic Data Archive: *Ecological Archives* E086-089-A5.