Effects of predatory ants on lower trophic levels across a gradient of coffee management complexity

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Summary

1. Ants are important predators in agricultural systems, and have complex and often strong effects on lower trophic levels. Agricultural intensification reduces habitat complexity, food web diversity and structure, and affects predator communities. Theory predicts that strong top-down cascades are less likely to occur as habitat and food web complexity decrease.

2. To examine relationships between habitat complexity and predator effects, we excluded ants from coffee plants in coffee agroecosystems varying in vegetation complexity. Specifically, we studied the effects of eliminating ants on arthropod assemblages, herbivory, damage by the coffee berry borer and coffee yields in four sites differing in management intensification. We also sampled ant assemblages in each management type to see whether changes in ant assemblages relate to any observed changes in top-down effects.

3. Removing ants did not change total arthropod densities, herbivory, coffee berry borer damage or coffee yields. Ants did affect densities of some arthropod orders, but did not affect densities of different feeding groups. The effects of ants on lower trophic levels did not change with coffee management intensity.

4. Diversity and activity of ants on experimental plants did not change with coffee intensification, but the ant species composition differed.

5. Although variation in habitat complexity may affect trophic cascades, manipulating predatory ants across a range of coffee agroecosystems varying in management intensity did not result in differing effects on arthropod assemblages, herbivory, coffee berry borer attack or coffee yields. Thus, there is no clear pattern that top-down effects of ants in coffee agroecosystems intensify or dampen with decreased habitat complexity.

Key-words: Chiapas Mexico, coffee agroecosystems, dominant arboreal ants, food web structure, intraguild predation.

Introduction

Modifications to habitat complexity may influence the top-down effects of predators, thereby changing how predators affect herbivores and plants. Changing habitat characteristics, such as refuge availability, may strongly affect predator–prey interactions, possibly affecting primary productivity. Experimental evidence from estuarine systems shows that increasing habitat complexity attenuates trophic cascades: predators have reduced effects in complex systems (Grabowski 2004). Further, increased predator diversity may dampen trophic cascades and limit the indirect positive effects of predators on

plants due to increased intraguild predation among predators (Sih, Englund & Wooster 1998; Finke & Denno 2004, 2005; Langellotto & Denno 2004). Yet predation by a diverse rather than single-species predator assemblage may more strongly decrease herbivore populations and increase plant yields (Cardinale *et al.* 2003). Diet complementarity among predators may increase overall effects on lower trophic levels (Duffy 2002; Hooper *et al.* 2005); however, effects of some complementary predators may be substitutable (Schmitz & Sokol-Hessner 2002). Increased prey diversity in complex habitats may dampen trophic cascades by either increasing plant consumption efficiency or increasing the proportion of unpalatable prey for predators (Duffy, Richardson & France 2005). Detangling effects of habitat complexity from related changes in food web structure and the number of trophic linkages is difficult. Some

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Table 1. Vegetation characteristics in four coffee agroecosystems differing in management intensity

Site†	TP	CP1	CP2	SM
Number of tree species	14	7·3	6·5	3
Number of tree individuals	44	31·9	47·2	15·3
Number of tree individuals >100 cm circumference	12·5	7	7	2
Percentage canopy cover	71·7	65·0	42·3	30·4
Percentage of sample points with shade from two species	10·3	10·6	0·7	1·0
Management index†	2·19	2·88	3·60	4·07

Vegetation was sampled in a series of 35×35-m plots in each site. See Philpott *et al.* (2006) for details.
†Sites are presented from left to right in order of increasing intensity. TP = traditional polyculture, CP1 = commercial polyculture site 1, CP2 = commercial polyculture site 2, SM = shade monoculture.
‡The management index is a scale from 0 to 5; higher management index values represent more intensive management. To calculate the index data for each vegetation variable were divided by the highest observed values to obtain a scale from 0 to 1 and then summed. Mean values for each site were compared using ANOVA. Values for each site are significantly different ($P < 0.05$).

food web theory predicts that trophic cascades should diminish as habitat and food web complexity is increased (Polis & Strong 1996), yet lower diversity and complexity may not be associated with stronger effects (Borer *et al.* 2005).

Coffee (*Coffea arabica* L.) agroecosystems provide a perfect natural setting for investigating whether changes in habitat complexity influence the effects of predators on lower trophic levels. Coffee was traditionally cultivated under diverse, dense shade canopies, but much current production is characterized by reduced vegetation complexity (Moguel & Toledo 1999). Coffee landscapes thus represent a patchwork of different management types following a gradient from floristically diverse and complex habitats resembling natural forests to systems where coffee is grown without a shade canopy. Complex coffee habitats have higher canopy cover, tree diversity, tree density, tree height and presence of epiphytic plants than do more simplified systems. Coffee intensification results in losses of diversity of herbivores and several predator groups, including arthropods and birds (Perfecto *et al.* 1996; Moguel & Toledo 1999; Philpott & Armbrecht 2006). Although many herbivores (>200 species worldwide) feed on coffee, complex coffee systems typically have few pest species, and some hypothesize that this is due to the diversity and abundance of predators found therein (Ibarra-Núñez 1990).

Ants are important generalist predators in natural and agricultural systems, including coffee agroecosystems (Way & Khoo 1992; Schmitz, Hamback & Beckerman 2000). Several ant species prey on insect pests, including the coffee berry borer (*Hypothenemus hampei* Ferrari), the most important coffee pest (Philpott & Armbrecht 2006). Ants also affect canopy arthropods in coffee plantations (Philpott *et al.* 2004), and prey on herbivores introduced into coffee farms (Philpott, Perfecto & Vandermeer 2008). Habitat complexity, ant diversity and complexity of ant interactions decline with coffee intensification (Perfecto *et al.* 1996; Moguel & Toledo 1999; Armbrecht 2003; Philpott & Armbrecht 2006), yet few authors have examined whether coffee habitat and food web simplification affects the impact of predators, such as ants, on lower trophic levels. Ants have stronger negative effects on coffee berry borers under high shade (complex habitat) management

than in sun coffee (Armbrecht 2003). The more widespread influences of ants on arthropod assemblages, plant damage or coffee yields under different coffee management strategies are unknown. We examined the function of ants as predators in coffee agroecosystems, and examined whether ant predation changes with management intensity. We tested whether (1) ants affect arthropods, herbivory or coffee yield; and (2) whether the top-down effects of ants change with changes in habitat complexity.

Methods

We eliminated ants from coffee plants in three large (300–1000-ha) coffee farms in the Soconusco region of south-west Chiapas, Mexico: (1) Irlanda (15°11′ N, 92°20′ W); (2) Hamburgo (15°10′ N, 92°19′ W); (3) Belen (15°15′ N, 92°22–23′ W). All farms are located between 950 and 1150 m elevation and receive 4500 mm rain per year. Belen contains two distinct management areas: a rustic or traditional management area (100 ha) and a production area (200 ha). We established ant exclosures in each of the two management types in Belen, with all study plots in Belen Rustic located at least 600 m from plots in Belen Production. Plots in Irlanda and Hamburgo were separated by a minimum of 1 km, and these were separated from plots in Finca Belen by 11 km. We thus established ant exclosures in four distinct study sites. In order of decreasing habitat complexity, Belen Rustic (TP) is a traditional polyculture, Irlanda (CP1) and Belen Production (CP2) are commercial polycultures, and Hamburgo (SM) is a shade monoculture (Moguel & Toledo 1999). The sites represent a gradient of coffee intensification and of habitat complexity whereby each site differs in overall floristic diversity and structure and pairs of sites differ for several vegetation characteristics (Table 1; Philpott, Perfecto & Vandermeer 2006). Sites were originally selected for use as replicate high-shade (TP and CP1) and low-shade (CP2 and SM) sites. However, because vegetation surveys revealed significant differences between the two high-shade and the two low-shade sites, we analysed ant effects in each site separately instead of including sites differing in vegetation complexity as replicate sites. Although this left only one site replicate per habitat, we are confident that study plots in different sites were distant enough from other sites (between 600 m and 11 km) to be independent.

In each study site, we established five replicate study blocks separated by at least 100 m. Each block consisted of two sub-blocks: one

in an area with a naturally occurring *Azteca instabilis* F. Smith colony; the other in an area 20 m away without an *A. instabilis* colony. We placed one half of the sub-blocks in areas near *A. instabilis* colonies because this ant is (a) the most abundant arboreal ant at the study sites; (b) distributed in patches; and (c) a likely keystone species in many trophic interactions (J.V. and co-workers, unpublished data). In each sub-block, we haphazardly selected four coffee plants and randomly assigned them to control (three plants) or no-ant (one plant) treatments. Blocks thus had eight plants (three with *A. instabilis* and other ants, three without *A. instabilis* but with other ants, and two without ants). The original study design included assigning one plant in each sub-block to a single-species nest-augmentation treatment and a second plant to a multiple-species nest-augmentation treatment. The ants in these nests did not survive, nor did their use augment ant activity, thus nest-augmentation plants were included as control plants for analyses. We excluded ants every 2 weeks by removing dry twigs and trunks, cutting arboreal connections, hand-removing ants, and placing Tanglefoot (The Tanglefoot Co., Grand Rapids, MI, USA) around coffee trunks, over wrapped flagging tape. On the same days, we gently shook control plants to control for any effects resulting from moving no-ant plants to cut arboreal bridges or to apply Tanglefoot. We maintained experimental treatments between coffee harvests from November 2000 to July 2001.

We sampled ants five times (November 2000, February, April, June and July 2001) to ensure ants were removed efficiently and to document the activity and species of any ants found on coffee plants. We placed tuna baits (*c.* 1 m height) on coffee plants, and identified all ants found on baits 20–30 min later. We recorded ant activity per species following an index (0 = no ants, 1 = 1–2 ants, 2 = 3–10 ants, 3 ≥ 10 ants) and summed across all species to calculate total ant activity per plant. We also examined total species richness per site and mean richness per plant to examine differences in the ant richness in each type of management system.

We sampled arthropods in June 2001, 8 months after establishing treatments. Over several days between 07.00 and 09.00 h, we sampled arthropods on two branches per plant (more than six leaves per branch) with a 10-cm-diameter reversed leaf-blower D-vac (WeedEater Co., Nashville, AR, USA). Arthropods were vacuumed into mesh bags, placed in sealed plastic bags and killed with ethyl acetate. We identified arthropods to order, and identified beetles to family so that they could be assigned later to feeding groups. We assigned arthropods to feeding groups (herbivore, predator, parasite, polyphage, detritivore) following Ibarra-Núñez *et al.* (2001). We measured the length and width of all leaves vacuumed, estimated leaf biomass using an empirically generated equation [biomass (g) = leaf area (0·025)–0·08], and standardized arthropod data as number of individuals per g foliage (I.P., unpublished data).

We sampled herbivore damage and coffee yields. We stratified coffee plants into three regions (top, middle and bottom of plants), and randomly selected one branch in each stratum to sample. We sampled herbivory when exclosures were established (November 2000), and on four subsequent dates (February, April, June, July 2001) by visually recording the percentage of leaf removed by chewing herbivores. We sampled herbivory on the 10 most apical leaves on the same branch on each sample date. Although damage by coffee leaf miners and sucking herbivores may be extensive in other regions (Borkhataria, Collazo & Groom 2006), damage caused by such herbivores is minimal at the study sites, and was not quantified. In July 2001, we counted the total number of fruits and the number damaged by the coffee berry borer on each sample branch. We calculated total yield by subtracting damaged fruits from the total per branch.

Some ants crossed Tanglefoot barriers, so we excluded from analyses all plants where ant activity exceeded 10 ants on any date (14 plants in total). We compared mean ant activity and richness on plants with and without ants (combining across sample dates) in different sites using ANOVA. We compared densities of common arthropods (>20 individuals collected) using two separate MANOVAs with either arthropod order (first test) or feeding group (second test) as the dependent variable, and treatment and site as main factors. Where MANOVAs were significant, we followed with ANOVAs for each order and feeding group. We excluded scale insects from MANOVAs because ants tend scale insects, thus we expected scale-insect densities to be much greater on control branches. We compared scale-insect densities using ANOVA. We examined differences in herbivory between ant treatment, sites and sample dates (February, April, June, July 2001) using repeated-measures ANOVA. The proportion of fruits damaged by the coffee berry borer, and total yields on plants with and without ants, were examined using ANOVA. We log-transformed data for herbivory and yield, and square-root transformed data for arthropods and damaged fruits to meet conditions of normality. Because of the unbalanced design and relatively low numbers of no-ant plants, we performed an *a posteriori* power calculation for the MANOVA, and ANOVAs examining herbivory, coffee berry borer attack, and yield.

Results

On average, ant activity was 25–35 times greater on plants with *A. instabilis* and other ants than on plants with only other ants or on plants without ants ($F_{1,143} = 48·074$, $P < 0·001$). Yet the presence of *A. instabilis* did not affect arthropods, coffee damage or yields. To simplify the results, we report here only two treatments: with ants or without ants. Ant activity and richness differed on plants with and without ants, but there were no differences between ant activity and richness in different sites (Table 2). Ant activity was from four to 10 times higher on plants with ants, signifying that exclosure treatments significantly restricted ant movement onto coffee plants (Table 2; $F_{1,138} = 96·098$, $P < 0·001$). Ant activity level did not differ among sites ($F_{3,138} = 0·541$, $P = 0·541$) and there was no interaction between ant presence and site ($F_{3,138} = 0·666$, $P = 0·574$). We collected 23 ant species in TP, CP1 and CP2, and 17 species in SM. All commonly encountered ant species (*A. instabilis*, *Pseudomyrmex* spp., *Crematogaster* spp.,

Table 2. Mean (±SE) ant species richness and ant activity index on coffee plants with ants and plants from which ants were removed in four coffee agroecosystems differing in management intensity

Site type	Species richness		Activity Index	
	Ants	No ants	Ants	No ants
TP	0·82 ± 0·07	0·05 ± 0·05	1·76 ± 0·19	0·05 ± 0·05
CP1	1·08 ± 0·08	0·11 ± 0·09	2·25 ± 0·19	0·09 ± 0·09
CP2	0·97 ± 0·07	0·24 ± 0·07	1·61 ± 0·14	0·12 ± 0·05
SM	0·85 ± 0·06	0 ± 0	2·09 ± 0·17	0 ± 0

Sites are in order of increasing intensity: traditional polyculture (TP), commercial polyculture (CP), shade monoculture (SM). A higher index value corresponds to higher ant activity.

Table 3. Mean (±SE) arthropods found on coffee plants with ants and plants from which ants were removed, and statistical differences based on ant presence, coffee sites with different management intensity, and interactions between ant presence and site

	Ants	No ants	Treatment d.f.	F	P	Site d.f.	F	P	Site × treatment d.f.	F	P
Total arthropods	0·699 ± 0·033	0·753 ± 0·147	1, 149	0·019	0·889	3, 149	3·030	**0·031**	3, 149	2·111	0·101
Scale insects	0·037 ± 0·006	0·111 ± 0·062	1, 149	6·404	**0·012**	3, 149	5·653	**<0·001**	3, 149	1·874	0·136
Arthropod orders			10, 140	2·439	**0·010**	30, 426	4·99	**<0·001**	30, 426	1·260	0·170
Acarida	0·020 ± 0·003	0·010 ± 0·003	1, 149	3·260	0·073	3, 149	3·833	**0·011**	3, 149	0·795	0·498
Aranae	0·057 ± 0·005	0·104 ± 0·054	1, 149	0·229	0·633	3, 149	7·499	**<0·001**	3, 149	2·515	0·061
Blattidae	0·010 ± 0·002	0·004 ± 0·002	1, 149	2·528	0·114	3, 149	0·308	0·820	3, 149	0·132	0·941
Coleoptera	0·038 ± 0·005	0·049 ± 0·011	1, 149	0·713	0·400	3, 149	3·601	**0·015**	3, 149	1·395	0·247
Collembola	0·043 ± 0·007	0·023 ± 0·008	1, 149	4·420	**0·037**	3, 149	12·394	**<0·001**	3, 149	0·218	0·884
Diptera	0·303 ± 0·019	0·238 ± 0·023	1, 149	1·597	0·208	3, 149	1·654	0·179	3, 149	0·687	0·562
Hemiptera	0·016 ± 0·003	0·021 ± 0·006	1, 149	0·804	0·371	3, 149	6·698	**<0·001**	3, 149	2·432	0·067
Hymenoptera	0·080 ± 0·007	0·076 ± 0·010	1, 149	0·005	0·943	3, 149	4·153	**0·007**	3, 149	0·578	0·630
Lepidoptera	0·002 ± 0·001	0·008 ± 0·003	1, 149	11·172	**0·001**	3, 149	3·736	**0·013**	3, 149	2·474	0·064
Orthoptera	0·008 ± 0·002	0·002 ± 0·001	1, 149	4·540	**0·035**	3, 149	0·964	0·412	3, 149	0·763	0·516
Feeding groups			5, 145	1·932	0·092	15, 441	4·723	**<0·001**	15, 441	1·053	0·399
Herbivore	0·289 ± 0·017	0·355 ± 0·081	1, 149	1·011	0·316	3, 149	8·993	**<0·001**	3, 149	1·576	0·198
Predator	0·079 ± 0·006	0·131 ± 0·054	1, 149	1·306	0·255	3, 149	5·385	**0·002**	3, 149	3·204	0·025
Polyphage	0·123 ± 0·051	0·039 ± 0·007	1, 149	2·659	0·105	3, 149	0·132	0·941	3, 149	0·445	0·721
Detritivore	0·132 ± 0·011	0·093 ± 0·011	1, 149	2·240	0·137	3, 149	1·769	0·156	3, 149	0·935	0·426
Parasite	0·118 ± 0·009	0·104 ± 0·012	1, 149	0·155	0·695	3, 149	2·696	**0·048**	3, 149	1·162	0·326

Arthropods are divided by order and by feeding strategy. Overall results for MANOVA tests for arthropod orders and feeding groups are located to the right of subheadings; individual ANOVA results correspond to individual orders or feeding groups. Bold values show significant differences.

Nesomyrmex spp., *Solenopsis* spp.) are functionally classified as generalist foragers and generalist predators (Brown 2000); no fungus cultivators or army ants were found on experimental plants. Mean ant richness per plant was significantly higher on plants with ants ($F_{1,138}$ = 106·143, P < 0·001), but ant richness did not differ with site ($F_{3,138}$ = 1·51, P = 0·215) and there was no interaction between ant treatment and site ($F_{3,138}$ = 0·417, P = 0·741).

Removing ants did not affect arthropod densities overall, or in specific sites. However, there were significant effects of removing ants on some arthropod groups for some sites (Table 3). Removing ants both increased and decreased densities of different arthropod orders, but did not affect any feeding group. Plants without ants had twice as many Lepidoptera, three times more scale insects, half as many Collembola, and four times fewer Orthoptera than plants with ants (Table 3). There were significant differences in densities of Acarida, Aranae, Coleoptera, Hemiptera, non-ant Hymenoptera, herbivores, predators and parasitic arthropods in different sites, but there were no significant interactions between site and ant-removal treatment.

Herbivory varied with site and date, but did not vary with ant presence (Fig. 1). Herbivory was twice as high in the TP site than in all the other coffee-management types (repeated-measures ANOVA, $F_{3,137}$ = 23·077·183, P < 0·001; Tukey's test, P < 0·001), but there was no effect of removing ants on leaf damage ($F_{1,137}$ = 0·638, P = 0·426) and no site × treatment interaction ($F_{3,137}$ = 0·545, P = 0·652), showing that ant effects on herbivory did not differ with management intensity. Herbivory did change with sample date ($F_{3,411}$ = 19·905,

P < 0·001). Although changes in herbivory over time did not vary by ant treatment ($F_{3,411}$ = 1·030, P = 0·379), changes did vary by site ($F_{9,411}$ = 3·160, P = 0·001). Ant presence did not affect berry borer attack or coffee yields (Fig. 2). Up to 18% of fruits per branch were attacked, but there were no effects of ant removal ($F_{1,132}$ = 0·014, P = 0·905), site ($F_{3,132}$ = 2·155, P = 0·096), or site × ant removal interaction on the proportion of damaged fruits ($F_{3,132}$ = 1·623, P = 0·187). The number of undamaged coffee fruits (yield) was higher in CP1 and SM than in TP and CP2 ($F_{3,138}$ = 12·322, P < 0·001), but there was no clear trend for yields to increase with decreasing shade. Furthermore, there was no effect of removing ants ($F_{1,138}$ = 1·672, P = 0·198) or an ant removal × site interaction ($F_{3,138}$ = 1·064, P = 0·366).

A posteriori power tests showed that, although many tests were of acceptable power despite low sample sizes, some tests may have increased type II error (Table 4).

Discussion

Overall, we saw relatively small impacts of removing ants in the four coffee agroecosystems of varying habitat complexity. The effects of ants on arthropods, herbivory and yields, in general, were much weaker than have been reported for many studies in agricultural and natural systems. In contrast to previous studies examining the effects of ants in agricultural and natural systems, ants did not affect herbivory, berry borer damage or coffee yields. Furthermore, there were no clear differences in the top-down effects of ants in sites along a gradient of habitat complexity. Overall, ants limited densities
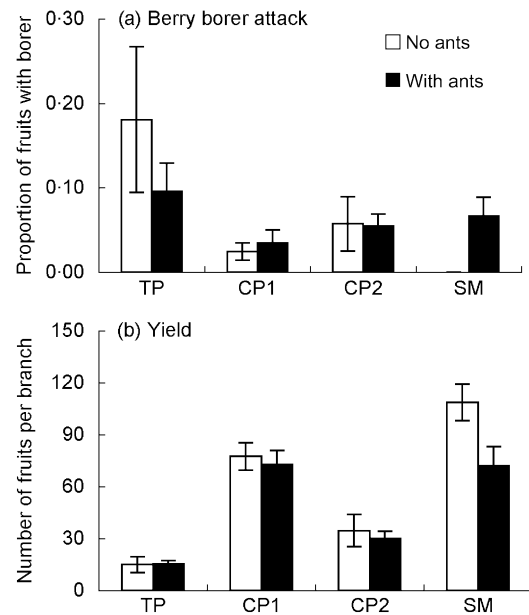
Table 4. Observed power of statistical tests for MANOVA to examine ant and site effects on arthropods, and ANOVA used to examine for site and treatment effects on herbivory, proportion of fruits with coffee berry borer, and coffee yield

Comparison	Site	Treatment	Site × treatment
Arthropod orders (all sizes)	1·000	0·934	0·952
Arthropod orders (small)	0·984	0·757	0·990
Arthropod feeding guilds (all)	1·000	0·640	0·690
Arthropod feeding guilds (small)	0·918	0·382	0·992
Herbivory	1·000	0·182	0·590
Berry borer damage	0·539	0·052	0·418
Coffee yield	1·000	0·250	0·283
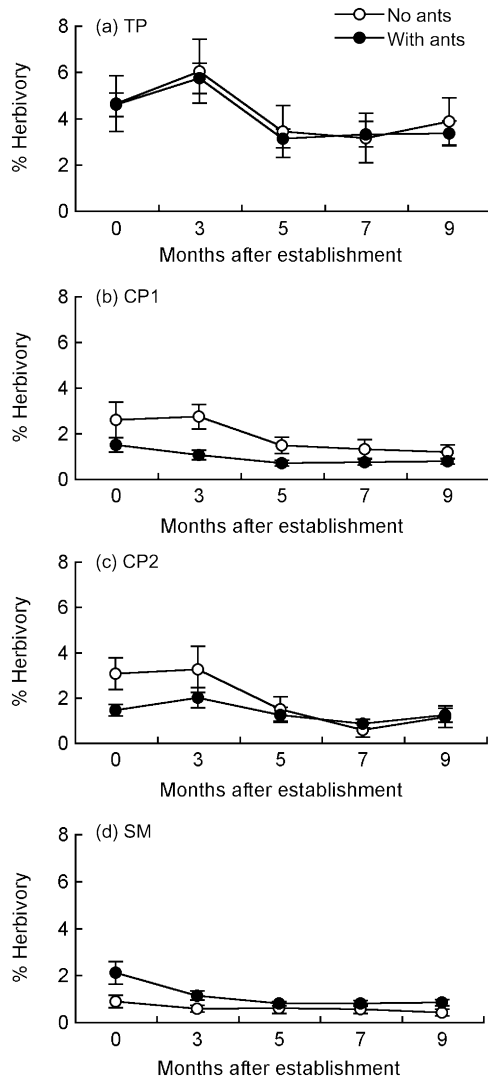
Fig. 1. Coffee herbivory on plants with and without ants in four sites varying in management intensity across five sample dates. Graphs are shown in order of increasing management intensity, where TP is a traditional polyculture, CP1 and CP2 are both commercial polycultures, and SM is shade monoculture. The least intensive site (TP) had significantly more herbivory than did the other three sites. See text for details. Bars, SE.

Fig. 2. Coffee damage and yield on plants with and without ants across four coffee sites varying in management intensity (least intensive on left). Bars, SE. Ant removal did not affect coffee damage or yields. There were significant site differences ($P < 0.001$) for yield but not for berry borer attack; there were no significant interactions between ant presence and site (see text for details).

of Lepidoptera, but densities of Orthoptera were higher on plants with ants. Thus ants may affect herbivore assemblages more strongly, rather than changing herbivore densities, and thereby may not alter the amount of herbivory caused by chewing herbivores. Interestingly, there were higher scale-insect

densities on plants without ants. This may be a result of using Tanglefoot to exclude ants. Tanglefoot is a non-selective removal agent and may have limited scale-insect emigration from plants without ants. Alternatively, high scale-insect densities may also be due to ants periodically harvesting hemipterans, especially when extrafloral nectar resources are available (as in *Inga* spp. canopy trees common in coffee plantations) (Ricogray 1993; Offenberg 2001).

There are several additional explanations as to why we did not observe strong top-down effects of ants in these sites. First, it is possible that ants are not important predators in coffee agroecosystems. However, many studies have documented that ants control several arthropod pests of coffee (Philpott & Armbrecht 2006). Second, in highly complex systems, predator effects tend to produce trophic cascades less frequently (Schmitz *et al.* 2000). The results of our study are consistent with this finding, as all coffee agroecosystem examined are relatively complex, each with upwards of 80 tree species, even in the simplest system examined. Ants are actively promoted by farmers to control pest populations in citrus and

coconut plantations, banana groves, sweet potato fields, and in corn, bean and squash systems because of the benefits ants provide to crop plants (Perfecto & Castiñeiras 1998). Yet the coffee systems examined here are all structurally and floristically much more complex than the tree plantations and annual crop systems mentioned above. Perhaps the habitat complexity in all our systems is too complex to allow us to notice any top-down effects of ants. Yet, in the same review of top-down effects of predators, ants influenced herbivore populations and plant biomass in 25 of 41 studies, many of which were conducted in tropical forest systems, thus presumably as diverse and complex as our sites (Schmitz *et al.* 2000). Nevertheless, ant effects on arthropod assemblages were not consistent across all arthropod orders. Other ant-exclusion studies similarly demonstrated both increases and decreases in densities of particular arthropod orders (Risch & Carroll 1982; James *et al.* 1999) or no effects on ground-foraging arthropods (Gibb 2003). In canopy trees in coffee farms, ants also have both positive and negative effects on several arthropod orders, depending on ant species and season (Philpott *et al.* 2004).

It is possible that predation by other predators may have increased in response to ant removal. Birds, lizards and spiders all have strongly negative effects on coffee arthropods and pests (Greenberg *et al.* 2000; Ibarra-Núñez *et al.* 2001; Borkhataria *et al.* 2006). There are strong intraguild interactions between ants and birds in these systems, such that ants reduce the foraging activity of birds in some trees (Philpott, Greenberg & Bichier 2005). Thus increased bird predation may have compensated for the removal of ants. Birds, lizards and spiders remove significantly more experimentally introduced herbivores on coffee plants from which ants have been removed than on plants with ants (Philpott *et al.* 2008).

Although some predict that top-down effects of predators and trophic cascades should diminish with increasing habitat complexity (Polis & Strong 1996), more recent reviews have found that many different factors determine the relative strength of trophic cascades (Borer *et al.* 2005). Although ants did have negative impacts on one important group of herbivores (caterpillars), we did not find strong overall effects of ants as top-down predators on arthropod assemblages, herbivory, or yield in coffee agroecosystems. This is despite the fact that ants are important predators in many simple agricultural systems and complex tropical forests. In sum, although ants may influence particular arthropods in coffee plantations, we did not find strong trends for top-down effects of ants, or for the effects of ants to decrease or increase in sites significantly varying in habitat complexity.

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