

PREDATORS, THEIR PREY, AND WHAT COMES BETWEEN THEM

Completing the Web in a Trophically Complex Coffee Agrosystem

Alex Bajcz¹

March 7th, 2010

Ivette Perfecto, Ph.D., Advisor

John Vandermeer, Ph.D., Reader

¹ University of Michigan – Ann Arbor, Michigan: Honors Program in the Environment

INTRODUCTION:

The tropics are home to two important entities: tropical ecosystems (which house an amazing amount of biodiversity) and many fast-growing export economies (which are converting those ecosystems into managed ones with alarming zeal). In many ways, coffee epitomizes this transformation (13, 2). Spurred by skyrocketing global demand, coffee production is intensifying at the expense of primary forest (13). However, shade-grown coffee, oft championed by conservationists, could be a best-of-both-worlds alternative, able to please both producers and consumers while providing viable refuge for dwindling tropical diversity (24, 17, 4, 13, 20, 2, and many others). Furthermore, shaded coffee systems might also provide a conduit for migration between forest fragments, forging a metapopulation structure that would facilitate landscape-wide conservation (23, 28, 29).

This diversity then gives back in the form of ecosystem services, valuable services performed by functional, healthy ecosystems, such as biological control of pests through top-down, or predator-driven, effects (22, 27, 26, 25, 13, 39, 2). Top-down control in complex systems often transcends simple predator-prey relationships; such systems sport a web structure, one in which intraguild (in this case, between predator) predation, as well as trait mediated effects—those effects which alter the rate at which predator-prey interactions occur—blur the linearity of the one-dimensional food chain (38). While viewing the trophic structure as a web of interactions can make teasing apart the net impacts of each individual predator more difficult, doing so is often more realistic and more enlightening (31, 23, 16, 27, but see 12).

Four predatory taxa that research has found critical to shade-coffee agrosystems are insectivorous birds (9, 22, 13, 39), bats (39), spiders (30), and Azteca ants (25, 26, 27). Some studies have even tried to study interactions between two or more of these groups (39, 26). However, we present the here-to-date first attempt at examining the entire predator guild at once. Once thought to be pests or liabilities, predators are now thought to be critical for maintaining low pest levels, and how factors such as predator diet breadth, prey diversity, predator habits and preferences, prey palatability and abundance, and intraguild predation alter the regulatory capacity of predators is now under increasing scrutiny (12, 33, 31). We argue that studying predators in these systems is paramount, not tangential, to conservation efforts (39).

One way to successfully attach a value to top-down control is to simply remove the predator(s) and observe the response of the lower trophic levels (12). If a predator exerts a strong top down control, we would expect a trophic cascade-- a “series of alternating positive and negative effects (33)”--to precipitate down through the trophic levels in its absence (for examples, see 1, 34).

After we observe (or don't observe) these cascading effects, we can begin to characterize the role of the predator. Of course, some caveats to this approach do exist. First, when intraguild

predation, omnivory, cannibalism, or non-hierarchical food webs characterize a system, predator effects can become blurry (1, 16, 13). For example, in addition to their predictable consumption of prey species, birds (31), spiders (6), and ants (26) are all known to engage in intraguild predation or trait mediated effects in this system: Birds and spiders are both known to eat ants on occasion (27, 10, but see 13, 2) and Azteca ants are thought to actively reduce bird foraging times (26, 27). Still, we feel predator removal experiments have a lot to offer studies of top-down control, especially when the study design addresses the entire predator guild.

In this study, our lab excluded all possible combinations of flying insectivores (birds and bats), spiders, and Azteca ants in order to elucidate their impacts on lower trophic levels in a shaded coffee agroecosystem. Birds and bats were excluded with fish netting over individual coffee plants, spiders were physically removed from coffee plants, and *Azteca instabilis*, a keystone arboreal and aggressive ant species (37) was spatially segregated by the experimental design. I then charted the responses of the arthropod assemblages on these plants over time. I addressed the following questions: (1) How much does each predator individually affect arthropod taxa positively and/or negatively? (2) How does the combination of predators affect arthropod taxa? How do they complement or interfere with one another? (3) Can we observe intraguild predation in this system? (4) Do we see evidence of top-down control in this system?

































METHODS:

Study Site and Data Collection

Finca Irlanda (15°11'N, 92°20'W; 900 m elevation; 4500 mm rain/yr) is a 300 hectare organic shade-coffee farm in the Soconusco region of Chiapas, Mexico (26). While structurally and biologically simpler than primary forest, *Finca Irlanda* has a high tree species diversity and is certified as Bird Friendly® by the Smithsonian Migratory Bird Center and as a Rainforest Alliance system. We selected fifteen plots without *A. instabilis* nests; we paired ten of these plots with nearby plots where Azteca were present. Within each plot, we subjected each of four adjacent coffee plants to one of four treatments: (1) control, (2) bird/bat exclusion, (3) spider removal, and (4) both bird/bat exclusion and spider removal. These four treatments, when coupled with Azteca presence or absence, make eight total treatments.

We excluded birds and bats using domed, hoop-like structures overlaid with a fine mesh that permitted arthropod movement but denied birds and bats access to the plant at all times. We manually removed spiders from treated plants at least weekly using an aspirator. Azteca presence was generally not actively controlled; however, when *A. instabilis* activity on target plants was low, small pieces of carton nests were placed on plants to maintain some level of ant activity. We collected arthropods during four months using a D-vac (a reverse leaf blower that collects arthropods on a fine mesh): September 2002 (wet season), December 2002 (dry), April 2003 (dry), and July 2003 (wet) (34). We collected all samples in early morning to minimize the loss of flying arthropods. We stored all specimens in a 70% ethanol solution and then typed them to the order and family level and measured them length-wise in millimeters.

Treatments

1				
2				
3				
4				
5				
6				
7				
8				

Data Analysis:

I entered and processed all arthropod data in Microsoft Excel. I focused on two response variables: arthropod abundance--the average number of arthropods of a given type per plant--and arthropod biomass--the average biomass in milligrams of an arthropod taxon per plant, both of which were compiled by date, site, and treatment.

I estimated biomass for each arthropod order using length-weight regression equations and Costa Rican rainforest coefficients presented in Schoener (1980) (32). I excluded all larval stages but included nymphal stages for those orders with coefficients for adults only. For orders with no published coefficients in Schoener (1980) (32), I used the average, "total" arthropod coefficients, which are based only on average data across all taxa and not on specific orders, so they may provide a poor estimate of true biomass. I calculated spider biomass using Amazonian spider coefficients presented in Höfer and Ott (11). Because biomass metrics change greatly with size, I treated spiders larger or smaller than 2.5 mm as two separate groups, using different coefficients for each (11).

My methodology includes both qualitative and statistical approaches. I conducted all statistical work using PASW 17 or Microsoft Excel, including: two-sample T-tests and Mixed Linear Regression Models (MLMs); One-way and Univariate ANOVAS; post hoc tests; and histograms, box-and-whisker plots, and scatterplots.

Both abundance and biomass varied strongly by sampling date. Additionally, sampling dates do not represent fully independent measures. For this reason, I used MLMs extensively to account for these limitations. These tests have less power than other tests do, so I used them chiefly when significant time effects were evident. Generally, when I used MLMs in concert with other, more standard tests, the p-values were similar. All statistical tests use an official alpha of 5%, though I consider those with p-values between 5-10% to be marginally significant.

To assess the roles of each predator individually, I recoded the original eight treatments into three diametric groups: (1) Birds/bats excluded/not excluded, (2) spiders removed/not removed, and (3) Azteca present/absent. These treatment codes look solely at whether the predator in question is present or absent, irrespective of the predator gradient in the background. That said, the effect shown by a given predator's treatment should reflect that predator's effect alone because the presence or absence of other predators will apply to both sides of each treatment.

I used these three treatments as explanatory variables for each arthropod taxon's abundance and biomass to determine any possible effect the predator has on them. I followed a five-step protocol. First, I removed outliers from the dependant variable (abundance or biomass) using box-and-whisker plots, removing only those outliers many standards deviations above the mean. Second, I used clustered histograms to assess the effect of the predator treatment on the dependant variable by date to ascertain directionality of an effect, if any. Third, I used One-Way ANOVAs to check for a time effect in the dependant variable. If I found a time effect, I used an MLM (Date and treatment within-subject fixed factors, plot between subjects random factor) to assess for a significant effect. If I did not find a time effect, I used both an MLM and a 2-Sample t-test and compared the results, reporting a significant result only if both tests found one. Lastly, I removed all zero values and re-ran the tests. I did this because a zero value for a plot may not actually represent an effect of the predator per se, but rather a simple absence of that taxon on that particular plant. In other words, a zero value is essentially interpreted by the test as "total extirpation due to treatment" when that may not be the case. Thus, for rarer taxa with many zero values, the mean becomes left-skewed, obscuring a predator's impact somewhat. These non-zero

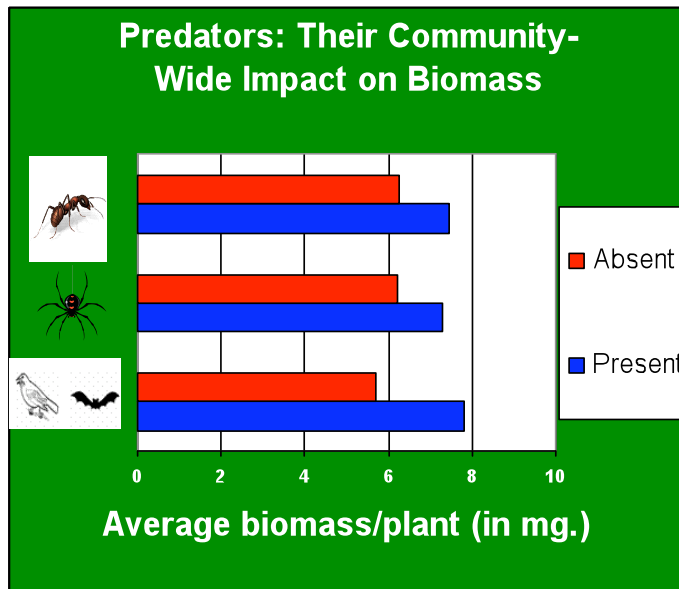
tests allowed me to more fully characterize each potential interaction of predator and prey, but significant results generally reflect a weaker association than those that include zero values.

I examined how predators interact to produce effects in two ways. First, I generated a percentage change table that shows how each predator duo affected specific taxa (Table 2). This table shows average percentage change from the predator-present state to the predator-absent state. Thus, a negative change means that the taxon has fallen by that percentage due to the predator's absence. Secondly, I used Univariate ANOVAs to reveal more complex interactions between the predators. In these tests, each of the three treatment codes, as well as the date, were used as fixed factors and full factorial models were assessed for significant results.

Two of the predators—spiders and Azteca—are potential prey themselves, and all three predators are thought to engage in intraguild interactions (34, 35, 36, 9, 25, 26, 27). The effects of flying insectivores on spiders and Azteca, as well as those of Azteca and spiders on each other, were assessed using a similar protocol to the one used to look at individual predator effects. However, for these groupings, the four treatments that weren't meant to contain the dependant predator were excluded from the analysis.

Lastly, I estimated the likelihood of top-down control in this system qualitatively through the extent to which the predators substantially affect their prey. I also present some graphs that show each predator's impact on the arthropod community as a whole (Figures 1 and 2). Finally, I present a theoretical interaction web, based on both the results from this study and those presented in the literature, to synthesize what is known about predators in this system thus far (Figure 4).

Figures 1 (above) & 2 (below): Arthropod Community Response to Predator Removal.



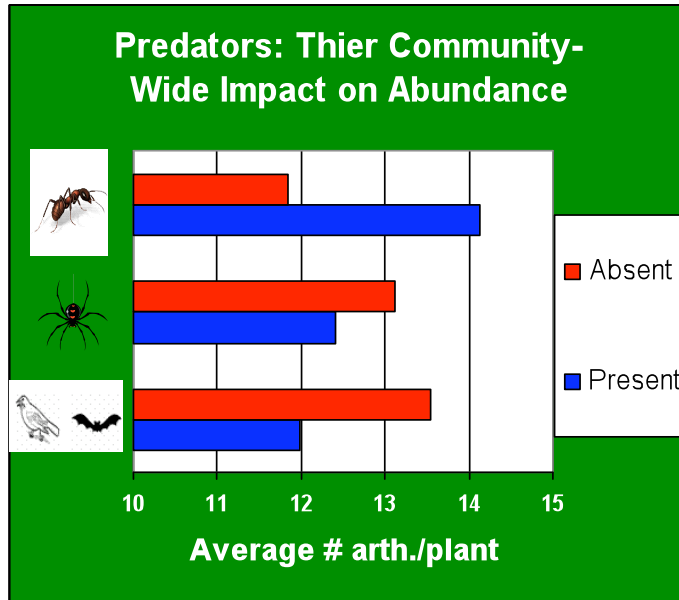
Shown is the arthropod community's response to predator removal in terms of average biomass (top) and average abundance (bottom).

RESULTS:

Descriptive Summary:

Non-Aztecan ants (Hymenoptera Formicidae) were excluded from all total abundance calculations due to excessive variability. Average arthropod biomass and average abundance did not vary significantly by site (for biomass, $F=1.402$, $df=393$, $p=.149$, for number

$F=.557$, $df=393$, $p=.897$), but biomass was found to vary by sampling date, with April ($p=0.017$) and July ($p=0.002$) significantly higher than September, on average. Abundance also varied significantly by date, with July being higher than September ($p=0.000$) or December ($p=0.004$) and April being higher than September ($p=0.013$).



Azteca were much more prevalent in treatments meant to contain Azteca (1.421 Azteca/plant) than in non-Azteca treatments (0.029 Azteca/plant). That said, spider abundance dropped just 14% in spider exclosure treatments (1.035 spiders/plant to 0.89 spiders/plant), even though spider biomass did drop 34% (1.70mg/plant to 1.13mg/plant), which suggests that spider removal may only have reduced the average size of spiders inhabiting treatment plants. Spider abundance may have been higher at the time of collection because weekly spider removal was not done concordantly with collection. Nonetheless, these results

indicate that the spider treatment did not result in full elimination of spiders as I may have hoped. I could not assess the effectiveness of bird/bat exclosures directly, but other experiments in this system have used similar exclosures with success (27, 9).

Individual Predator Effects:

Table 1 shows all significant effects of individual predator absence on taxa I found using my statistical regiment. Birds/bats exclosure resulted in a significant increase in total arthropods, spiders, Azteca ants, orthopterans, collembolans, mites (Acarida) and scale insects (Coccidae). For total arthropods and scale insects, only abundance showed this relationship and for mites only biomass did. In contrast, bird/bat exclosures resulted in a significant decline in abundance and biomass of flies and beetles and the decline in the abundance of parasitic hymenopterans. These data are available in Tables 1 and 2. I also tested for a seasonal dimension of bird/bat exclosure for when the migratory birds were present (December 2002 and April 2003) and absent (September 2002 and July 2003). As Figure 3 shows, only Orthopterans show a seasonal response.

Azteca absence correlated with a significant rise in the biomass and abundance of mites and the biomass of thrips (Thysanoptera). Additionally, Azteca absence coincided with a drop in total arthropod and fly biomass as well as spider abundance (Tables 1 and 2). Finally, spider removal correlated with a significant increase in beetle abundances and homopteran biomass (Tables 1 and 2).

I have also summarized all individual predator effects into a percentage change table using all taxonomic groups with 200+ individuals in the dataset, regardless of whether the change is significant or not (Table 2). This table compares the percentage change of a taxon's average abundance or biomass as the predator is excluded, removed, or absent; a negative (red) value shows a loss of biomass or abundance as the predator becomes absent, suggesting the predator's presence may be beneficial in some way. A green value represents a decline in abundance or biomass due to the predator's absence.

Table 1: Significant Predator Effects on Target Taxa

Predator Effects	Taxa	Test	Direction	P-value	Sig.?	Test Type	Notes
<u>Bird/Bat Exclosure</u>	Coccidae	Abundance	Positive	0.039	Yes	MLM	
	Arthropods**	Abundance	Positive	0.037	Yes	MLM	
	Araneae	Biomass	Positive	0.074	Marginal	MLM	All plots only.
	Araneae	Abundance	Positive	0.023	Yes	2S T-test	Spider plots only.
	Azteca	Abundance	Positive	0.001	Yes	MLM	Azteca plots & no zeros only
	Azteca	Biomass	Positive	<0.001	Yes	MLM	Azteca plots & no zeros only
	Parasitoids***	Abundance	Negative	0.007	Yes	2S T-test	
	Orthoptera	Abundance	Positive	<0.001	Yes	MLM	
	Orthoptera	Biomass	Positive	0.038	Yes	MLM	All plots only.
	Diptera	Abundance	Negative	<0.001	Yes	MLM	
	Diptera	Biomass	Negative	<0.001	Yes	MLM	
	Acarida	Abundance	Positive	<0.001	Yes	MLM	
	Acarida	Biomass	Positive	0.0085	Yes	MLM	
	Collembola	Biomass	Positive	0.039	Yes	MLM	
	Coleoptera	Abundance	Negative	<0.001	Yes	MLM	
	Coleoptera	Biomass	Negative	<0.001	Yes	2S T-test	
<u>Azteca Absence</u>	Araneae	Abundance	Negative	0.0085	Yes	MLM	Spider plots only.
	Arthropods**	Biomass	Negative	0.0385	Yes	MLM	
	Thysanoptera	Biomass	Positive	0.0485	Yes	MLM	
	Diptera	Biomass	Negative	0.0455	Yes	2S T-test	
	Acarida	Abundance	Positive	0.0045	Yes	MLM	
	Acarida	Biomass	Positive	0.0105	Yes	MLM	
	Collembola	Abundance	Positive	0.0935	Marginal	MLM	Possible false positive.
	Coleoptera	Abundance	Negative	0.0795	Marginal	MLM	No zeroes only.
	Coleoptera	Biomass	Negative	0.056	Marginal	2S T-test	
<u>Spider Removal</u>	Thysanoptera	Abundance	Negative	0.057	Marginal	2S T-test	All Apr. plots only.
	Acarida	Biomass	Negative	0.0795	Marginal	MLM	
	Collembola	Biomass	Positive	0.0695	Marginal	MLM	
	Coleoptera	Abundance	Positive	0.0145	Yes	MLM	No zeroes only
	Homoptera	Biomass	Positive	0.031	Yes	2S T-test	

Shown are the statistically significant results of individual predator treatments. Direction indicates the effect predator absence had on the taxon listed. Marginal results are included in this table for completeness.

Table 2: All Predator Effects on Taxa Represented by Percentage Change.

Abundance	Total	Coccidae	Arth. > 5.0mm	Arth. > 3.0mm	Azteca	"Parasitoids"	Spiders
<u>Birds/Bats Exclosure</u>	13.11%	29.29%	-18.64%	16.38%	146.38%	-30.00%	63.91%
<u>Spider Removal</u>	5.81%	10.74%	37.78%	-30.58%	-31.69%	12.28%	-33.71%
<u>Azteca Absence</u>	-16.17%	-49.12%	-14.89%	-18.43%	-97.99%	-12.27%	1.29%
Abundance	Acarida	Coleoptera	Collembola	Diptera	Homoptera	Orthoptera	Thysanoptera
<u>Birds/Bats Exclosure</u>	72.03%	-35.13%	59.52%	-45.91%	36.11%	79.27%	-28.89%
<u>Spider Removal</u>	-27.11%	-6.91%	69.14%	-2.42%	16.03%	0.88%	-2.56%
<u>Azteca Absence</u>	115.30%	-14.12%	67.74%	-24.64%	-39.04%	-19.87%	74.90%
Biomass	Total	Coccidae	Arth. > 5.0mm	Arth. > 3.0mm	Azteca	"Parasitoids"	Spiders
<u>Birds/Bats Exclosure</u>	-26.91%	N/A	N/A	-18.75%	163.31%	-30.48%	42.22%
<u>Spider Removal</u>	-14.84%	N/A	N/A	-25.64%	-31.78%	-5.43%	-14.06%
<u>Azteca Absence</u>	-16.22%	N/A	N/A	-16.84%	-97.99%	17.28%	-15.73%
Biomass	Acarida	Coleoptera	Collembola	Diptera	Homoptera	Orthoptera	Thysanoptera
<u>Birds/Bats Exclosure</u>	95.45%	-47.42%	55.74%	-65.92%	-7.69%	14.62%	-15.15%
<u>Spider Removal</u>	-27.03%	2.70%	47.62%	5.42%	33.84%	-32.01%	-3.23%
<u>Azteca Absence</u>	115.79%	-41.20%	16.90%	-35.23%	24.67%	-31.20%	54.35%

Shown are percentage changes of average biomass or abundance per plant following removal, absence or exclosure of a given predator. A negative or red value means that that predator's absence lowered the taxa by the percentage shown, while a positive or green value shows the opposite trend.

Predator Interaction Effects

Often, the effect of one predator differs from the effect of the other, so each predator's relative importance in creating the overall effect we observe can be ascertained, to some degree, by the arthropod community's response to each predator separately and both predators in concert. Between-predator interactions are presented in Table 3. This table shows percentage change of arthropod abundance across the range of both predators' presence and absence. These results are complex, as are the interactions that underlie them, and while I have not run statistics on these comparisons, I present them here to make these results accessible for later work.

Univariate ANOVAs revealed some instances where all three predators combined to significantly alter the final arthropod abundance of a taxon. Additionally, these tests showed some instances where the two predators interacted with both each other and the collection date, implying their interaction changed in nature over time. Significant results are included in Table 4. Other significant interactions between at least one predator and the date or two predators are as follows: Arthropod Biomass-Spiders & Azteca (F: 3.253, p=0.072); Arthropods >3.0mm-Azteca & Date (F:2.545, p=0.056); Orthoptera abundance- Date & Birds (F: 2.498,p=0.059), Birds & Azteca (F: 2.874,p=0.091), Spiders & Azteca (F: 2.733, p=0.099); Diptera biomass-Birds & Azteca (F: 4.315, p=0.038); Acarida abundance- Birds & Azteca (F: 3.036, p=0.082); and Coleoptera biomass- Date & Azteca (F: 2.465, p=0.062). Date interacted with nearly every treatment for almost every predator, so I do not report any two-or-fewer predator interactions that did not at least interact with the date as well, although I acknowledge that interactions that aren't time sensitive may very well exist.

Table 3: Two-Predator Interactions on Taxon Abundance by Percentage Change

Spiders Vs. Azteca	Total	Coccidae	Collembola	Thysanoptera	Parasitoids	Acarida	
Neither Present	12.583	3.517	1.083	0.583	0.683	1.283	
Spiders Present	7.68%	-2.39%	-53.83%	60.03%	7.32%	45.52%	
Azteca Present	43.05%	135.29%	-49.22%	-14.24%	-37.77%	-57.13%	
Both Present	-16.36%	-26.07%	-60.76%	-27.10%	-12.15%	-31.80%	
Birds/Bats Vs. Azteca	Total	Coccidae	Spiders	Orthoptera	Thysanoptera	Diptera	
Neither Present	12.583	3.517	1.017	0.717	0.538	0.450	
Birds/Bats Present	-12.18%	-36.96%	-19.67%	-72.11%	134.48%	29.56%	
Azteca Present	43.05%	135.29%	-9.05%	1.12%	-14.24%	-22.22%	
Both Present	-3.44%	-15.41%	-23.80%	8.09%	-35.68%	150.00%	
Spiders Vs Birds/Bats	Total	Arth.>3.0mm	Parasitoids	Orthoptera	Thysanoptera	Acarida	Diptera
Neither Present	12.583	3.25	0.683	0.717	0.583	1.283	0.45
Birds/ Bats Present	-12.18%	-7.17%	17.13%	-72.11%	134.48%	-36.32%	29.56%
Spiders Present	7.68%	18.46%	7.32%	9.21%	60.03%	45.52%	-14.89%
Both Present	-18.94%	138.98%	43.92%	-46.58%	42.88%	-23.38%	66.67%

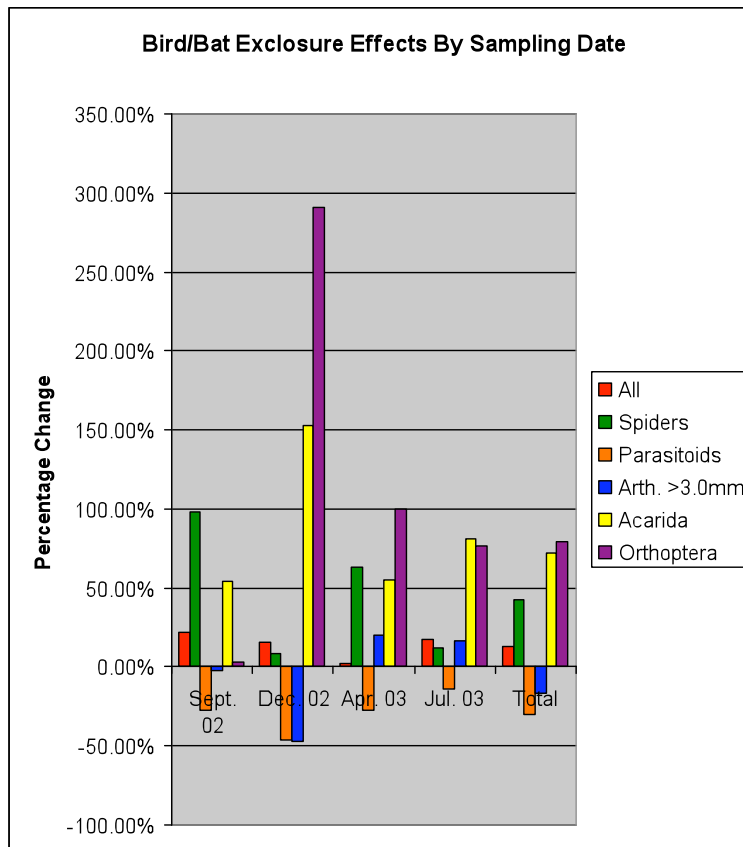
Shown is the percentage change from the control (neither predator present) of average arthropod abundance (given in white as arthropod number per plant) as predators are sequentially "added." Directionality is the same as Table 2.

Table 4: *Specific Taxon Responses to Interacting Predator and Time Effects*

Complex Interactions	Sept. 02	Dec. 02	Apr. 03	Jul. 03	Total
Parasitoids					
...after Spider Removal	48%	-23%	-32%	-18%	-12%
...where Azteca Absent	-45%	65%	23%	21%	12%
Orthopterans					
...after Spider Removal	25%	45%	0%	-29%	1%
...where Azteca Absent	-17%	-17%	-17%	-24%	-20%
Diptera					
...after Spider Removal	20%	8%	-29%	-15%	-2%
...where Azteca Absent	-29%	-35%	29%	-31%	-25%
...where Birds/Bats Excluded	-39%	-40%	-68%	-43%	-46%
Scale Insects					
...after Spider Removal	-15%	44%	-2%	8%	11%
...where Azteca Absent	-27%	46%	82%	-76%	-49%
Arthropods >3.0mm					
...where Birds/Bats Excluded	-3%	-47%	20%	17%	-16%
Coleoptera					
...where Azteca Absent	-27%	-49%	1%	27%	-14%
Araneae					
...where Azteca Absent	-34%	-50%	23%	-74%	-16%

Shown are percentage changes, presented as comparisons within each sampling date. As such, effects of date are compartmentalized for rapid comparison. These results show that many individual effects of a given predator are effectively cancelled out by the opposite effects of another.

Figure 3: *Bird/Bat Exclusion Effects and Seasonality*



Shown is the percentage change of various taxa across all sampling dates with respect to bird/bat exclusion. Thus, a positive value indicates a positive response to bird/bat exclusion. Only Acarida and Orthoptera show strong responses in the migratory bird season (Dec. & Apr.) vs. the rest of the year, suggesting they may be preferentially preyed on by migratory birds.

DISCUSSION:

Individual Predators: Who's Eating Who

This study verifies the results of many other exclusion studies that show birds and bats cause a decline in the abundance and biomass of the arthropod community (34, 13, 9, 27, 26, 36,

but see 2). The positive effect bird/bat enclosure had on spiders is particularly notable as probable intraguild predation (34, 2, 31). However, birds/bats still managed to limit total arthropods despite also reducing spiders, particularly the orders Orthoptera and Acarida. This differs somewhat from Polis et. al.'s (1989) suggestion that prey abundance will increase as intraguild predation reduces the prevalence of the subordinate predator (here, spiders), though other studies with bird/bat enclosures have found similar results in tropical ecosystems (9, 34, 31).

Philpott (2004) observed that birds significantly reduced the population of Orthopterans, spiders, ants, mites, and collembolans, all of which I observed in my study as well. In addition, Diptera, Coleoptera and non-formicid Hymenoptera all benefited from the presence of birds/bats. Because these taxa are common prey of spiders, top-down regulation of spiders by birds could explain this observation (35). Unfortunately, my results for spider removal do not validate this conclusion. While spider removal resulted in the expected decline in beetle biomass, I observed no effect on beetle abundance or Diptera and non-formicid Hymenoptera abundance and biomass. That said, the spider removal treatment was not very effective at eliminating spiders, turning my "spider removal" treatment into, at best, a "spider reduction" treatment, which could explain the few significant effects that were found for spiders in this study overall.

Some researchers have only found birds to exert strong top-down control in similar systems during the wet season (34) or for larger or certain arthropod prey only (Greenberg 9, 34, 18, 27, but see 36). In contrast, my results show fairly consistent bird and bat enclosure effects across seasons (with a few exceptions) that are not particularly sensitive to size effects. Migratory patterns are known to affect insectivorous bird presence in coffee agrosystems—one reason such systems are lauded for their conservation value (13, 39, 35). In my study, migratory bird impacts, if any, are only observed in Orthopterans, who suffer disproportionately from birds/bat presence during December and April when migratory birds are present (Figure 3). Otherwise, the direction and intensity of bird effects varied limitedly across most taxa. I did not observe any effects of birds/bats on large arthropods, though I suspect this could be due to my study's paucity of such organisms ($107_{\text{large}}/6605_{\text{total}}$).

William-Guillen and colleagues (2008) found that the effects of birds are often confounded by the effects of bats in "bird enclosure" experiments (39); if the enclosures are left up through the night, they also exclude bats. Although my original design was meant to exclude only birds, I have decided to deem my treatments "bird/bat enclosures" to avoid the risk of attributing bat effects to birds. In truth, the work of William-Guillen et. al. (2008) found that while birds are the dominant flying insectivore in winter in this coffee system due to the influx of migratory birds, bats are dominant the rest of the year. This interplay between birds and bats may have led to a dilution of seasonal effects in this study. Interestingly, in my study, only orthopterans and acarida responded positively to winter bird/bat enclosure, suggesting birds, not bats, are these taxa' primary predator.

Spiders reduced the biomass of coleopterans and homopterans, as well as collembolan biomass marginally, which are all reasonable prey species for spiders (34). Spiders also marginally increased the abundance of thrips and mites in this system, though the reasons for this are unknown. Overall, many spider effects were strong but not significantly so. Notably, I didn't observe any significant increase in non-formidicae hymenoptera (parasitoids). Spider removal showed few results in my study. I can think of a couple of reasons to explain this. First, spider removal may simply have been ineffective. Second, spiders are known to participate in cannibalism, so a rise in spider prevalence could have been tempered by increased spider-spider

predation (31). Third, spiders and parasitoids theoretically compete for a similar prey pool, so the removal of spiders could have been cancelled out by a rise in parasitism, although my data doesn't necessarily lend support to this hypothesis (16, 2). Additionally, parasitoid abundance was not controlled in my study, so I have no way of assessing for any potential compensation that they may perform when spiders are absent. Lastly, spiders, despite their generalist nature, may show prey preference; camouflaged or well defended prey may, for example, proliferate while spiders are present, but other types of arthropods may do better in a spider-free area, making the net effect of spiders nearly zero (12, 34, 15, 19).

Azteca had negative impacts on acaridans, collembolans, and thysanopterans and positive effects on spiders, dipterans, and coleopterans. Overall, arthropod abundance and biomass were much lower when Azteca were absent, suggesting that Azteca presence supports a larger arthropod community. Philpott et. al. (2008) have posited that Azteca presence doesn't necessarily effect either herbivory or primary productivity, so they may not exert as strong of top-down control as other predators (25). I believe that my results, which show effects of Azteca on many taxa, make these assertions worth reconsidering. Additionally, Blüthgen et. al. (2000) concluded that due to their dependence on homopteran honeydew for calories, aphid-tending ant genera such as Azteca may not be "predators" in the classical sense at all but rather specialist, keystone herbivores (3). While the body of research conducted in *Finca Irlanda* suggests this conclusion may be hasty for coffee agrosystems, I believe examining this assertion in greater detail would be worthy (see 25).

Predators Combine to Effect Prey

Table 3 presents many results that are not necessarily significant, so I concede any analysis of its patterns must be taken with a grain of salt because any pattern could conceivably have arisen by chance. Still, publishing these results makes them available to fuel future hypotheses more focused on predator interactions in coffee systems.

First, Azteca and spiders each seem to reduce the arthropod community on their own but have little effect when acting in concert; they seem to be interfering with each other in some manner. The mechanism for this interference, if it exists, is unknown. One particularly interesting example of their interference is over parasitoids; in each of the four months surveyed, Azteca and spiders impacted parasitoids strongly in opposite directions. Additionally, their interference seems to vary in intensity and direction over time and across different taxonomic groups and levels. Indeed, at this time, this relationship seems exceedingly complex. Overall, I believe these results show that the interplay between spiders and Azteca may help strengthen the vibrancy of the arthropod community in these systems.

Birds/bats and spiders appear to show a less balanced relationship. The net impact of both predator groups together appears to be consistently in the direction of birds/bats acting alone for nearly every taxon (though not large arthropods) and the only variable appears to be the intensity of this relationship. Generally, the effects of birds/bats overshadow those of spiders. I don't find this trend surprising because generalist predators, such as spiders, have been shown to cause consistently lower effects on prey species volume or biomass while specialist predators, such as birds, often show larger effects (1, but see 12).

Lastly, Azteca and birds seem to interfere with one another in some manner. That said, while some of the results regarding the two taxa make intuitive sense (e.g. scale insects and spiders), other results seem wildly out of sync (diptera, thysanoptera, and orthoptera). I have no

explanation for these phenomena at this time, but they certainly pinpoint a potential gap in our knowledge of this system.

Intraguild Predation and Predator-Predator Interactions

I have no way of assessing whether spiders or Azteca antagonized birds but spiders are not known to do so. However, birds and spiders seem to compete for Orthoptera (Table 3) and may compete for other species as well. Conversely, birds reduce spider abundance and biomass significantly (Table 1), and Azteca can keep birds from foraging on branches where they are tending scale insects (26, 31). Total average arthropod abundance drops by less due to birds when Azteca are present (Table 3). On the other hand, birds reduce Azteca abundance and biomass significantly (Table 1), but they also seem to reduce the abundance of the scale insects upon which Azteca are dependant (Table 2) (26). Lastly, spiders and Azteca seem to have a complex relationship. Azteca definitely increase the prevalence of spiders where they are present (Table 1). Otherwise, Azteca may facilitate the hunting habits of spider for some prey (for example, collembola and thysanoptera), even while inhibiting them from hunting other prey types (for example, parasitoids) (but see 10).

<http://resources1.news.com.au/images/2008/03/16/va1237297168095/Isla-Fisher-Supplied-5939228.jpg> Birds, spiders, and Azteca all substantiated their roles as both predators and competitors in this system. As competitors in particular, they almost certainly directly impacted each other. Spiders and Azteca suffered at the hands of birds/bats, while spider and Azteca abundance both fell by 33% when the other was absent, suggesting some sort of fraternity between them (26). Because spiders and ants may compete for similar prey, may forage in the same areas, and may be observed to visibly harass one another, this result is hard to explain (19, 10). Because spiders occasionally eat Azteca, Azteca may “help” spiders by providing an

additional, and sometimes plentiful, backup food source (10). Another possible explanation is simply that Azteca and spiders may not compete as actively for food resources as previously thought (3). Also, ant-bird antagonism could benefit spiders in this system; if Azteca lower bird foraging times, consumption of spiders by birds could be lower where Azteca are present (10, 26). How Azteca might benefit from spiders, on the other hand, is unclear to me at this time.

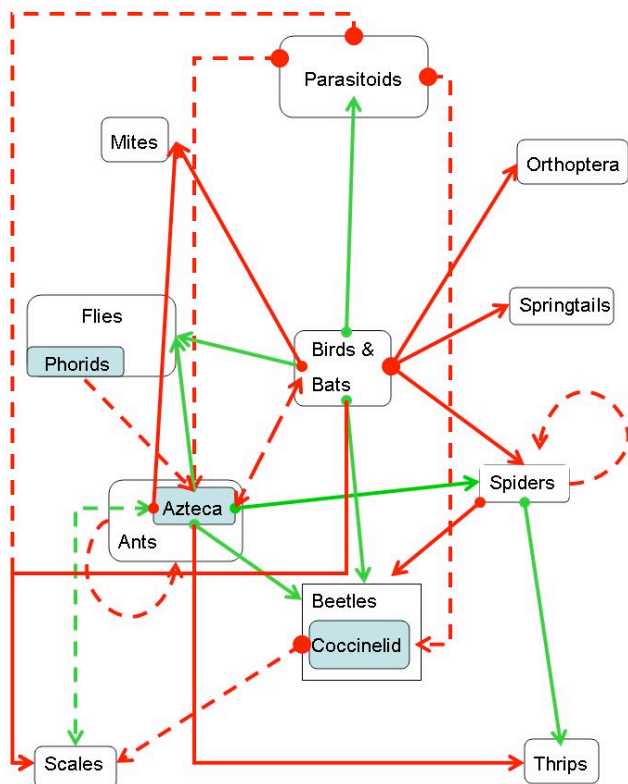


Figure 4: The Updated Interaction Web

Shown is my interpretation of the interaction web of this system, based on my own findings and those of other researchers. The solid arrows are my own results and dashed arrows are attributed to previous researchers. Red arrows denote negative effects on the receiving taxa while

green arrows denote positive effects (23, 25, 26, 27, 34, 39).

Predators and the Stability of the Ecosystem

Biomass of arthropods in this coffee system undeniably went down as predators were removed (Figure 1). Predator removal has been shown to cause a drop in biodiversity, which could cause one or a few prey species to expand at the expense of others and bring about lower system biomass (12). Biomass may also drop as predators are removed because the vast intricacy of the system requires predators, underscoring the potential importance of maintaining predators during system management (23). Figure 4 shows what I believe to be the properly updated interaction web of this system, based on both my own research and results attested in the literature.

Although I have no way of measuring cascade strength directly, I believe my results reflect the high likelihood of a cascade in this system if predators were removed. Birds/bats and Azteca ants caused the abundance or biomass of many taxa to rise or fall, (usually) in concert with previous conceptions of this system's trophic hierarchy (23, 25, 26, 27, 34, 39). For example, bird/bat presence coincided with a drop in spiders, a parasitoid expansion, and an arthropod community reduction, reflecting an apparent four-tier trophic hierarchy that could be disrupted by the exclusion of birds and bats (33, 6, 39). Secondly, systems in which the herbivores are predominantly invertebrates, like this system, often have stronger cascades because these herbivores capitalize more quickly and efficiently on predator release than vertebrate herbivores (1). Additionally, endothermic vertebrates, such as birds and bats, have been known to cause particularly strong cascades, possibly due to their large caloric intake (1). I conclude that looking for a trophic cascade in this system as they are industrialized would be a valuable research endeavor.

However, proving a trophic cascade in this system may be difficult for a few key reasons. First, cascades are often tempered in systems where plant chemical defenses are strong, which is certainly the case for coffee (1). Cascade strength can also be inversely proportional to diversity because higher diversity lessens each predator's specific impact and stabilizes the system as a whole (6, 1, 25). Lastly, coincidental intraguild predation (predators eating insects that are infected with parasitoids) is likely in this system and can noticeably obscure cascading effects (31, 7, 16).

Future research in this system should focus on a few key points. First, I agree with Memmott et. al. (2000) that parasitoids need to be examined concurrently with predators to properly delineate their interrelationships (16). While parasitoid removal might prove unwieldy, a parasitoid introduction ("flooding") could be employed instead. Also, I agree that studies on trophic cascades and top-down regulation need to be conducted in a more varied set of terrestrial ecosystems, although I would argue that shade coffee and cocoa agroecosystems are still good options (1). Lastly, Philpott et. al. (2008) examined predator effects by sorting arthropods into feeding groups, made possible by our better collective understanding of the system's biota (25). With that knowledge in hand, a fresh repeat of this experiment could make these results more solid, thorough, and broadly applicable.

Lastly, it's important that projects like this one continue to emphasize the value of traditional, shade-grown, and organic coffee systems in the face of ever-increasing agricultural intensification in the tropics. These systems are rich in biodiversity and are havens for migratory birds and other endangered biota (34, 9, 24, 17, 13, 39). Thus, pressure to maintain the complexity and vibrancy of these systems should increase, especially to protect predators, which

are often the first taxonomic levels to be extirpated by intensification (25, 34), and parasitoids, which are often ideal agents of organic, biological pest control (5, 7). Over the long run, losing these systems to intensification may come at a cost to sustainability and biodiversity too great for the world to bear.

CONCLUSION:

The relative importance of spiders, Azteca ants, and insectivorous birds and bats were assessed in a shade coffee agrosystem. During the process of analysis, birds were found to negatively impact both other predators and many prey taxa, while Azteca ants and spiders only seemed to affect specific taxa under certain conditions. Also, many suppositions made about the trophic structure of the system were confirmed or, at the very least, substantiated by statistical evidence: (1) birds do negatively affect spiders; (2) while spiders were not found to have a significant effect on parasitoid abundance per se, bird removal did decrease parasitoid numbers, suggesting a possible indirect effect through spiders; (3) Azteca and spiders do interact, though not necessarily in the ways we've previously thought; (4) Azteca and birds may in fact display intraguild competition; (5) predators do seem to be important enough to the stability of the ecosystem that their removal could cause significant rises in the arthropod herbivores beneath them, potentially leading to increased pest outbreaks; (6) coffee agroecosystems are structurally and taxonomically complex; (7) many of the interactions between different taxonomic levels vary seasonally and spatially, leading to less consistent distinctions of one taxa being uniformly "good" or "bad" for another.

ACKNOWLEDGEMENTS:

I'd like to thank, first and foremost, my advisor, Dr. Ivette Perfecto, for the opportunity to work on this fascinating project, in addition to the wealth of guidance, support, and interest she's shown me. Thanks also to Dr. Bobbi Low, who faithfully steered me through the dark waters of indecision and uncertainty. Special thanks to Dr. John Vandermeer for offering me his perspective and extensive knowledge of Agroecology as well as his time. Thanks to the University of Michigan CSCAR office for helping me through my statistical dark ages, to my fellow Honors students for their moral support and friendliness, to James Le Moine for his feedback, and to Dr. Brenda Gunderson for her willingness to help point me in the right direction. You all are the foundation upon which I hope I have built something special.

LITERATURE CITED:

1. Borer, E. T., E.W. Seabloom, J.B. Shurin, K.E. Anderson, C.A. Blinchette, B. Broitman, S.D. Cooper, and B.S. Halpern. "What Determines the Strength of a Trophic Cascade?" *Ecology* **86**:528-537. 2005.
2. Borkhataria, Rena, R., Jaime A. Collazo, and Martha J. Groom. "Additive Effects of Vertebrate Predators on Insects in a Puerto Rican Coffee Plantation." *Ecological Applications* **16**: 696-703. 2006
3. Blüthgen, Nico, Manfred Verhaagh, William Goitia, Klaus Jaffe, Wilfried Morawetz, and Wilhelm Barthlott. "How plants shape the ant community in the Amazonian rainforest

- canopy: the key role of extrafloral nectarines and homopteran honeydew.” *Oecologia* **125**:229-240. 2000.
4. Donald, Paul F. “Biodiversity Impacts of Some Agricultural Commodity Production Systems.” *Conservation Biology* **18**: 17-37. 2004.
 5. Eilers, Elisabeth Johanna and Alexandra-Maria Klein. “Landscape context and management effects on an important insect pest and its natural enemies in almond.” *Biological Control* **51**:388-394. 2009.
 6. Fagan, William F. “Omnivory as a Stabilizing Feature of Natural Communities.” *The American Naturalist* **150**:554-567. 1997.
 7. Force, Don C. “Ecology of Insect Host-Parasitoid Communities.” *Science* **184**:624-632. 1974.
 8. Greenberg, Russell, Ivette Perfecto, and Stacy M. Philpott. “Agroforests as Model Systems for Tropical Ecology.” *Ecology* **89**:913-914. 2008.
 9. Greenberg, Russell, Peter Bichier, Andrea Cruz Angon, Charles MacVean, Ronaldo Perez, and Enio Cano. “The Impact of Avian Insectivory on Arthropods and Leaf Damage in Some Guatemalan Coffee Plantations.” *Ecology* **81**: 1750-1755. 2000.
 10. Halaj, J., D.W. Ross, and A.R. Moldenke. “Negative effects of ant foraging on spiders in Douglas-fir canopies.” *Oecologia* **109**:313-322. 1997.
 11. Höfer, Hubert and Ricardo Ott. “Estimating biomass of Neotropical spiders and other arachnids (Araneae, Opiliones, Pseudoscorpiones, Ricinulei) by mass-length regressions.” *Journal of Arachnology* **37**(2):160-169. 2009
 12. Jiang, Lin and Peter J. Morin. “Predator Diet Breadth Influences the Relative Importance of Bottom-Up and Top-Down Control of Prey Biomass and Diversity.” *The American Naturalist* **165**:350-363. 2005.
 13. Johnson, Matthew D., Natalee J. Levy, Jherime L. Kellerman, and Dwight E. Robinson. “Effects of shade and bird exclusion on arthropods and leaf damage on coffee farms in Jamaica’s Blue Mountains.” *Agroforestry Systems* **76**: 139-148.
 14. Klein, Alexandra-Maria. “Nearby rainforest promotes coffee pollination by increasing spatio-temporal stability in bee species richness.” *Forest Ecology and Management* **258**: 1838-1845. 2009.
 15. Lang, Andreas, Juliane Filser, and Johannes R. Henschel. “Predation by ground beetles and wolf spiders on herbivorous insects in a maize crop.” *Agriculture, Ecosystems and Environment* **72**:189-199. 1999.
 16. Memmott, J., N.D. Martinez, and J.E. Cohen. “Predators, parasitoids and pathogens: Species richness, trophic generality and body sizes in a natural food web.” *Journal of Animal Ecology* **29**:1-15. 2000.
 17. Moguel, Patricia and Victor M. Toledo. “Biodiversity Conservation in Traditional Coffee Systems of Mexico.” *Conservation Biology* **13**: 11-21. 1999.
 18. Moorman, Christopher E., Liessa T. Bowen, John C. Kilgo, Clyde E. Sorenson, James L. Hanula, Scott Horn, and Mike D. Ulyshen. “Seasonal diets of insectivorous birds using canopy gaps in a bottomland forest.” *Journal of Field Ornithology* **78**(1):11-20. 2007.
 19. Nentwig, Wolfgang. “Prey analysis of four species of tropical orb-weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone.” *Oecologia* **66**:580-594. 1985.
 20. Perfecto, Ivette, Inge Armbrrecht, Stacy M. Philpott, Lorena Soto-Pinto, and Thomas V. Dietsch. “Shaded coffee and the stability of rainforest margins in northern Latin America.” *Stability of Tropical Rainforest Margins: Linking Ecological, Economic and*

- Social Constraints of Land Use and Conservation. Eds. Tscharntke T; Leuschner C; Zeller M; Guhardja E; Bidin A. Springer-Verlag: Berlin. 2007. 227-263
21. Perfecto, Ivette, Inge Armbrecht, Stacy M. Philpott, Lorena Soto-Pinto, and Thomas V. Dietsch. "Shaded coffee and the stability of rainforest margins in northern Latin America." *Stability of Tropical Rainforest Margins: Linking Ecological, Economic and Social Constraints of Land Use and Conservation*. Eds. Tscharntke T; Leuschner C; Zeller M; Guhardja E; Bidin A. Springer-Verlag: Berlin. 2007. 227-263
 22. Perfecto, Ivette, John H. Vandermeer, Gustavo Lopez Bautista, Guillermo Ibarra Nunez, Russell Greenberg, Peter Bichier, and Suzanne Langridge. "Greater Predation in Shaded Coffee Farms: The Role of Resident Neotropical Birds." *Ecology* **85**: 2677-2681. 2004.
 23. Perfecto, Ivette and John Vandermeer. "Spatial Pattern and Ecological Process in the Coffee Agroforestry System." *Ecology* **89**:915-920. 2008.
 24. Perfecto, Ivette, Robert A. Rice, Russell Greenberg, and Martha E. Van der Voort. "Shade Coffee: A Disappearing Refuge for Biodiversity." *BioScience* **46**: 598-608. 1996.
 25. Philpott, S. M., I. Perfecto, and J. Vandermeer. "Effects of predatory ants on lower trophic levels across a gradient of coffee management complexity." *Journal of Animal Ecology* **77**:505-511. 2008.
 26. Philpott, Stacy M., Russell Greenberg, and Peter Bichier. "The Influence of Ants on the Foraging Behavior of Birds in an Agroforest." *Biotropica* **37**(3): 468-471. 2005.
 27. Philpott, Stacy M., Russell Greenberg, Peter Bichier, and Ivette Perfecto. "Impacts of major predators on tropical agroforest arthropods: comparisons within and across taxa." *Oecologia* **140**:140-149. 2004.
 28. Pineda, Eduardo, Claudia Moreno, Federico Escobar, and Gonzalo Halffter. "Frog, Bat, and Dung Beetle Diversity in the Cloud Forest and Coffee Agroecosystems of Veracruz, Mexico." *Conservation Biology* **19**: 400-410. 2005.
 29. Pineda, Eduardo and Gonzalo Halffter. "Species diversity and habitat fragmentation: frogs in a tropical montane landscape in Mexico." *Biological Conservation* **117**: 499-508. 2004.
 30. Pinkus-Rendon, Miguel Angel, Jorge Leonel Leon-Cortes, and Guillermo Ibarra-Nunez. "Spider diversity in a tropical habitat gradient in Chiapas, Mexico." *Diversity and Distributions* **12**: 61-69. 2006.
 31. Polis, Gary A., Christopher A. Myers, and Robert D. Holt. "The Ecology and Evolution of Intraguild Predation: Potential Competitors That Eat Each Other." *Annual Review of Ecological Systems* **20**:297-330. 1989.
 32. Schoener, Thomas W. "Length-Weight Regressions in Tropical and Temperate Forest-Understory Insects." *Entomological Society of America* **73**:106-109. 1980.
 33. Terborgh, John, Lawrence Lopez, Percy Nunez V., Madhu Rao, Ghazala Shahabuddin, Gabriela Orihuela, Mailen Riveros, Rafael Ascanio, Greg H. Adler, Thomas D. Lambert, and Luis Balbas. "Ecological Meltdown in Predator-Free Forest Fragments." *Science* **294**:1923-1925. 2001.
 34. Van Bael, Sunshine A., Jeffrey D. Brawn, and Scott K. Robinson. "Birds defend trees from herbivores in a Neotropical forest canopy." *The Proceedings of the National Academy of Sciences* **100**:8302-8307. 2003.
 35. Van Bael, Sunshine A., Peter Bichier, and Russell Greenberg. "Bird predation on insects reduces damage to the foliage of cocoa trees (*Theobroma cacao*) in western Panama." *Journal of Tropical Ecology* **23**:715-719. 2007.

36. Van Bael, Sunshine A., Stacy M. Philpott, Russell Greenberg, Peter Bichier, Nicholas A. Barber, Kailen A. Mooney, and Daniel S. Gruner. "Birds as Predators in Tropical Agroforestry Systems." *Ecology* **89**:928-934. 2008.
37. Vandermeer, John, Ivette Perfecto, and Stacy M. Philpott. "Clusters of ant colonies and robust criticality in a tropical agroecosystem." *Nature* **451**: 457-459. 2008.
38. Werner, Earl E. and Scott Peacor. "A Review of Trait-Mediated Indirect Interactions in Ecological Communities." *Ecology* **84**: 1083-1100. 2003.
39. Williams-Guillen, Kimberly, Ivette Perfecto, and John Vandermeer. "Bats Limit Insects in a Neotropical Agroforestry System." *Science* **320**: 70. 2008.