Project Title: Investigating the effects of shade canopy management on natural enemies, pests, plant damage, and yield in organic coffee plantations

Principal Researcher:
Dr. Stacy M. Philpott
Department of Environmental Sciences, University of Toledo
2801 W. Bancroft St., Toledo, Ohio, 43606 USA
Telephone: 419-530-2578; E-mail: stacy.philpott@utoledo.edu

Farmers:
Mr. Bernd Peters and Mr. Walter Peters
Finca Irlanda
7A. Oriente S/N, Local 5, Entre 13 Y 15 Av. Norte, Tapachula, Chiapas 30700, Mexico
Telephone: 01-52-1-962-642-6508
E-mail: bpeters_60@yahoo.com

1. Project Summary

Many conservation organizations and ecologists have promoted organic, shade coffee farming as a direction towards agroecosystem sustainability and protection of tropical biodiversity. Coffee was traditionally grown under a native shade tree canopy, and ecological studies demonstrate that organic, shade-grown coffee provides much-needed habitat for migratory birds, mammals, and arthropods. However, in the past 40 years, agronomists have consistently advised farmers to intensify coffee systems, leading to the removal of shade trees and adoption of agrochemical use to boost production and diminish problems with pests and fungal diseases. Conventional farms do experience some increases in productivity but, from an ecological standpoint, there is still much debate about possible trade-offs between short-term increases in yields and the long-term consequences of intensification. Furthermore, little is known about how the simplification of the shade canopy (e.g. removal of trees, reduction in the diversity of shade tree species, and loss of canopy cover) will affect arthropod populations, predator-prey interactions, plant damage, and crop yield in organic coffee farms, in particular.

We investigated the impacts of shade tree thinning in an organic coffee plantation in southern Mexico. Specifically, we examined how farmer-motivated changes in shade management influence arthropods in the farm including natural enemies and herbivores and how changes in shade management affected levels of plant damage and yields. The objectives of the research were to: 1) determine the effect of shade canopy removal on abundance and diversity of natural enemies and on herbivorous pests in organic coffee plantations, 2) determine effect of shade canopy removal on coffee plant damage (e.g. herbivory, fungal disease, coffee leaf mines, fruits attacked by the berry borer), 3) determine the effect of canopy removal on coffee yields, and 4) disseminate information about biodiversity and ecosystem services in relation to canopy management to farmers, farm workers, farmer organizations, research institutions, and certification agencies.

Several measured factors differed with shade management type. We found significant differences in vegetation, not surprisingly, with more trees, more tree species, larger and taller trees, and more canopy cover in the uncut area compared with the cut areas. Thus, vegetation complexity was

reduced by the shift in the shade management regime. The shift in the shade did not have large effects on arthropods, overall, but arthropods were abundant and diverse in the farm. We found a total of 9328 individuals from 18 orders and found 39 families of beetles. We found no change in abundance of herbivores, predators, decomposers, beneficial arthropods, the ratio of herbivores to beneficial arthropods, spiders, beetles, parasitoid wasps, or caterpillars in the three habitat types. There were, however, several seasonal changes in arthropod abundance and a few differences between sites during certain months. More specific surveys of two natural enemies (ants and spiders) did reveal some differences. Ants were diverse in the farm, representing 47 species. There were more ant species in the area cut in 2008 and in the uncut area compared with the area cut in 2007. Ant abundance was greater in the uncut area and the area cut in 2007, and spider abundance was higher in the area cut in 2007 than in the area cut in 2008. Thus, specific taxa of natural enemies appeared to be either more diverse or more abundant in more undisturbed habitats.

There were larger differences in plant damage and yield between habitats. There was more fungal disease caused by ojo de gallo in the uncut habitat and more herbivory. Further, there was more accumulation of fungal diseases (ojo de gallo and leaf rust) in the uncut area and twice as much herbivory accumulation. However, amounts of leaf damage were extremely low throughout the farm even if differences were statistically significant. There was more damage caused by the coffee berry borer, with twice as much damage in uncut areas. Finally, coffee yields were twice as high in the cut areas, both in terms of total fruits produced and fruit weight. Thus, in this study, we documented both higher presence of natural enemies and higher damage in the uncut habitats, and higher yields in the cut habitats. It appears, based on the findings of this study, that traditional polycultures without shade management are less productive than commercial polyculture habitats with pruning. Taken together with previous studies, there is likely a trade-off between yields and biodiversity protection in organic coffee agroecosystems managed as in the studied farm.

This work contributes to our knowledge of organic coffee farming practices for several reasons. First, we lack vital basic information about the ecological responses of coffee agroecosystems to changes in shade management. The project provides some necessary information for making ecologically informed decisions on this particular farm. Outreach activities will make the findings available to farmers in Chiapas as well as in other coffee-producing countries. Second, the research provides the foundation for more specific studies related to ants, spiders, and parasitoid wasps – all important biological control agents. Thus, the work provides a framework for further investigation about pest management in organic coffee farms. Third, there is a general movement in Mexican and in international organic certification organizations to include criteria relevant to shade management in coffee farms as part of organic certification. There are also growing movements for double certification including both shade and organic certification of coffee farms. From a standpoint focused only on biodiversity, there is ample evidence that shade trees are beneficial, but before these systems are further promoted and adopted by farmers in Chiapas and elsewhere, a detailed investigation of the effects of shade trees on natural enemy and herbivore populations, plant damage, and coffee yields is necessary. Our work provides information about potential trade-offs between shade and coffee yields and will inform certification programs.

2. Introduction to Topic

Managed agricultural systems and human settlements make up to 95% of the world land area (Western & Pearl 1989, Pimentel *et al.* 1992) and are important in biological conservation and ecosystem sustainability. In Mexico, coffee accounts for 669,000 hectares of cultivated land (Perfecto *et al.* 1996). Traditional or shade-grown coffee agroecosystems house a high diversity of migratory birds (Greenberg *et al.* 2000) and predatory arthropods (Perfecto *et al.* 1997, Ibarra-Nunez 1990). Maintaining shade trees provides other benefits such as controlling soil erosion, fixing nitrogen, reducing weeds, and crop diversification (Beer 1987). Nonetheless, many coffee farmers convert their farms to sun-grown coffee or cut significant numbers of trees on their farms with the intent to increase crop yields (Soto-Pinto *et al.* 2000). These technified plantations often use agrochemicals, negatively impacting coffee workers and the environment (Agne 2000). Convincing Mexican coffee farmers, roughly 85% of which currently maintain shaded coffee plantations (Perfecto *et al.* 1996), that shade trees are important biologically and environmentally is crucial for maintaining biodiversity of resident and migrant species in this sub-tropical region.

Coffee (*Coffea arabica*) was traditionally cultivated under diverse shade canopies but recent production is characterized by intensive systems lacking shade trees (Coyner 1960, DeGraaf 1986). Such intensification results in losses of predator diversity (Swift *et al.* 1996), often equating with ecosystem instability, namely pest outbreaks (Elton 1958, Root 1973, Schulze & Mooney 1993, Losey & Denno 1999). Traditional coffee systems, though supporting a high diversity of herbivores, do not typically have large pest problems (Le-Pelley 1973) perhaps due to a high predator diversity maintaining potential pests at low population levels (Ibarra-Nuñez 1990). Increased predator diversity may also translate into higher functional richness, meaning that pest control may be more efficient within diverse agroecosystems (Flynn *et al.* 2008). Predator diversity in coffee farms could also function under the 'insurance hypothesis', described from theoretical systems (Yachi & Loreau 1999, Ives *et al.* 2005), where diversity contributes to long-term stability when environmental conditions change, as they inevitably do (Chesson & Case 1986).

Although recent work has focused on biodiversity and ecosystem services in coffee agroecosystems (see reviews and meta-analyses by Perfecto *et al.* 2007, Philpott *et al.* 2008, Van Bael *et al.* 2008), it is not clear how shade management of organic coffee farms will affect predator and prey populations and diversity, pest and disease damage, and yields within coffee farms. Farmers often operate under the conventional wisdom that decreased shade in farms will increase yields, but the ecological literature relating coffee shade to yield is highly mixed. Furthermore, studies in organic cropping systems, in general, investigate predator diversity and compare organic to conventional systems but relatively few make connections with predator-prey ratios, crop damage, and yields (Letourneau & Bothwell 2008). In coffee agroecosystems, there are significant loses of diversity of natural enemies (e.g. ants, spiders, parasitoid wasps) where management is intensified (Perfecto *et al.* 1996, Perfecto & Vandermeer 1996, Perfecto & Vandermeer 2000, Armbrecht *et al.* 2005, Philpott *et al.* 2006). Furthermore, several predators (e.g. ants, spiders, birds) control the coffee berry borer (Velez *et al.* 2003, Perfecto & Vandermeer 2006, Armbrecht & Gallego 2007, Kellermann et al. 2008) and the coffee leaf miner (Lomeli-Flores 2007, De la Mora *et al.* 2008), the two most important coffee pests. These services may be enhanced in systems with more shade cover (e.g. Armbrecht & Gallego 2007) or where functional or behavioral diversity of predatory species is maintained (Van Bael *et al.* 2008, Philpott *et al.* 2008). What is still incompletely understood, however, is how management changes, and specifically shade tree removal from coffee agroecosystems, affects the entire suite of arthropods including various functional groups (natural enemies including predators and parasitoids and herbivores), the ratio of natural enemies to herbivores in coffee agroecosystems, and how such changes may relate to level of insect damage and yields in coffee farms.

We examined how drastic changes in shade management of one large organic coffee farm in southern Mexico have affected the arthropods, damage, and yields on the farm. Our research focused on understanding the impact of drastic reductions in farm canopy cover on the abundance and biodiversity of arthropod functional groups (e.g. natural enemies, herbivores) on predator-prey ratios within the farm, on herbivore- and fungus-related plant damage, and on coffee yields.

Traditional coffee plantations in Mexico were managed with a shade canopy but, beginning in the 1970's with funding from the Mexican government, IMNECAFE, a coffee extension organization, began a widespread program to promote removal of forest and canopy trees and gradual replacement with nitrogen-fixing legumes and deciduous canopy trees. These techniques were largely promoted as part of green revolution techniques, that together with improved crop varieties and increased chemical and fertilizer inputs would improve coffee yields. However, many of the ecological interactions affected by shade tree removal were left unstudied, and it is now well recognized that eliminating the shade in coffee farms also removes important components of the associated biodiversity. Although the conventional wisdom of coffee farmers and of extension agents is that reducing the shade will increase yields and reduce problems with fungal diseases, the ecological realities of these assumptions have not be widely tested in an experimental setting. Nor is it clear that removing shade will have benefits for organic plantations where other green revolution techniques (e.g. nitrogen fertilizers to take the place of biological fixation, or herbicides to take care of the expected surge in weed growth) cannot be used. The issues are important to organic producers because although yield is an important outcome, so is ecological sustainability. Losses of biodiversity and decreases in ecosystem services (pollination, pest control, protection from erosion, resistance to the effects of hurricanes) have all been demonstrated to be greater in shaded farms than in farms where shade trees are removed (Perfecto *et al.* 2007). We examined in a detailed fashion the implications of shade cutting for arthropod abundance and diversity and explicitly tested implications for plant damage (by herbivores, fungal diseases, and fruit borers) and to coffee yields.

The research was conducted at Finca Irlanda, an organic certified coffee farm. Farmers were involved in the research. In 1967 Finca Irlanda became the first farm certified as organic and biodynamic by Demeter. The farm is currently certified biodynamic by Demeter and is organically certified by IMO Control, OCIA, and JAS OCIA. The farm also holds shade certification from the Rainforest Alliance and Bird-Friendly Certification from the Smithsonian Migratory Bird Center. Farmers were involved in the project by starting the shade experiment to examine impacts on their coffee yields. They have welcomed researchers on their farm for the past 15 years and have been involved in actively assessing the impacts of their management strategies on biodiversity within their farm. During this process, they were involved in conducting the large-scale management experiment; researchers followed up by collecting data on arthropods, damage, and yield.

3. Objectives Statement

The proposed research aimed to understand the impact of drastic reductions in shade canopy cover on the abundance and biodiversity of arthropod functional groups, on herbivore-related plant damage, and on coffee yields. The specific objectives of the research were to:

A. Determine the effect of shade canopy removal on abundance and diversity of natural enemies (e.g. ants and spiders) and on herbivorous pests (e.g. caterpillars and coffee green scale) in organic coffee plantations.
B. Determine effect of shade canopy removal on coffee plant damage (e.g. herbivory, coffee leaf mines, fungal disease lesions, fruit attack by the coffee berry borer).
C. Determine the effect of canopy removal on coffee yields.
D. Disseminate information about biodiversity and ecosystem services in relation to canopy management to farmers, farm workers, farmer organizations, research institutions, and

certification agencies.

The project will advance organic coffee farming because understanding the influence of shade management is essential in this agroecosystem. Coffee evolved under a shade canopy, and coffee quality is reportedly improved where coffee is grown under shade. However, many extensionists and farmer cooperatives have in the past promoted removal of the shade to manage yields, fungal diseases, and pests. The ecological knowledge relating to these management changes remains understudied. Furthermore, current certification of organic coffee, at least in the case of Certimex in Mexico, includes criteria relating to the shade canopy and management, pruning, or removal of trees. A better understanding of the ecological interactions between shade management, natural enemies, pests, and yield is important both for understanding long-term sustainability of organic coffee farms and making recommendations for organic certifiers that certify coffee.

4. Materials and Methods

Experimental design:

The project was conducted at Finca Irlanda, a 280-hectare organic shaded coffee plantation in the Soconusco region of Chiapas, Mexico (15°11´N, 92°20´W). The farm is 40 km NW of Tapachula. Finca Irlanda is 900 m above sea level and receives 4500 mm of rain per yr. The farm contains several management areas due to a recent drastic management change. Prior to 2007, the farm contained two management areas: 1) a traditional polyculture area with high canopy cover and diversity and density of shade trees (~8 hectares), and 2) a commercial polyculture with lower levels of canopy cover, tree diversity and density (~240 hectares). In May 2007, approximately 1/2 of the commercial polyculture was heavily pruned resulting in a drop in tree density from ~240 to ~120 trees per hectare in the cut area. In May 2008, the other 1/2 of the commercial polyculture area was pruned.

Our experimental set-up took advantage of these three distinct management areas: 1) uncut traditional polyculture, 2) commercial polyculture cut in 2007, and 3) commercial polyculture cut in 2008 (Fig. 1) to examine the impact of shade tree removal on natural enemies, herbivores, and coffee yield. In each management area, we established 25 plots, each separated by at least 50 m (Fig. 2). Within each plot we sampled vegetation, arthropods, plant damage, and coffee yields. Each plot consisted to two coffee plants, selected to be relatively similar in size (height, branches, total number of leaves) and coffee variety.

Local environmental factors:

In each plot, we surveyed vegetation in a 20 x 20 m plot surrounding the pair of coffee plants. We counted, identified, and measured height and circumference of each tree. We also took 5 canopy cover measurements in the center and 10 m to the N, S, E, and W of the plot with a convex vertical densiometer. We also examined the fraction of trees in the genus *Inga*, a nitrogen-fixing legume commonly planted in coffee farms in the study region. We compared mean values in the different habitats with multivariate ANOVA including number of individuals, number of *Inga* spp. individuals, number of species, mean circumference, mean tree height, and canopy cover as dependent variables. A significant MANOVA was followed by univariate ANOVA to determine differences in individual factors. Values for the number of individuals and number of *Inga* spp. individuals were log (ln + 1) transformed to meet conditions of normality.

General arthropod sampling:

To sample the arthropod community in the different coffee management areas, we used a D-VAC vacuum sampler to aspirate arthropods from coffee leaves. Four times during the year (July 2009, October 2009, February 2010, and June 2010) we sampled two branches on each coffee plant with a D-VAC aspirator between 5:30-7:30 AM. Following aspiration, we marked the two branches and returned the following day to measure the length of each leaf. We then used an empirically generated equation to estimate leaf width (width = 1.761(length) + 0.773) and then estimated leaf area using the area formula for an ellipse (Area = length / 2 x width / 2 x Pi). During each subsequent sample month, we sampled two new branches.

To examine the effects of shade management on arthropod abundance for certain groups, we identified all arthropods collected to order (e.g. Hemiptera, Coleoptera) and some (beetles) were further identified to family. We categorized each arthropod order or family to a functional class (predator, parasite, herbivore, decomposer) to determine impacts on herbivores relative to beneficial arthropods. All arthropod data were examined as number of individuals per leaf area sampled. We compared the abundance of different orders and functional groups sampled with ANOVA with management type and date as main factors. Arthropod densities were all log (ln + 1) transformed to meet conditions of normality. We also examined the herbivore to beneficial arthropod (H:B) ratios in different systems and examined for correlations between H:B ratios and canopy cover.

Natural enemies:

For a more in-depth sampling of natural enemies, we directly sampled ants and spiders. We sampled ants using tuna fish baits (1 g) placed on the main stem of each coffee plant approximately 1.5 m above ground once each month for the duration of the experiment. After placing baits, we waited for 30 min. and returned to collect all ants seen. All tuna was removed immediately following sampling to not influence the populations of ants or other arthropods in the study plants. Ants were identified to genus and to morphospecies or species where possible. We examined species richness of ants using species accumulation curves created with EstimateS. Spiders were sampled using visual searches on each plot. We visually searched plants for arthropods each month during the year. Visual searches lasted 5 min. per plant for a total of ~17 hours of sampling each month. We here report data only for spiders for the months of July 2009, October 2009, February 2010, and April 2010. Spiders were not identified, however, we examined spider abundance in the different habitat types. We originally intended to collect caterpillars during all activities to take to the lab and rear for parasitoids; however, caterpillar abundance was extremely low and thus we did not examine parasitoid abundance or diversity in this manner.

Herbivores:

We also did directed surveys for one coffee herbivore. We counted the number of scale insects (*Coccus viridis*) present on the stems, leaves, and fruits of two branches per coffee plant (Fig. 3e). Branches will be marked and the same branches will be sampled during the 1-year sample period. We assessed the abundance of other coffee pests indirectly by examining plant damage (see below).

Plant damage:

We examined four main categories of plant damage: 1) lesions caused by two fungal diseases, the coffee leaf rust (*Hemileia vastatrix*) and ojo de gallo (*Mycena citricolor*), 2) leaf mines caused by the coffee leaf miner (*Leucoptera coffeella*), 3) leaf herbivory due to chewing herbivores, and 4) fruit damage caused by the coffee berry borer (*Hypothenemus hampei*)(Fig. 3a-d, f). We sampled leaf damage on two randomly selected branches per plant, one in the top half of the plant and the other in the bottom half of the plant. We marked the underside of all leaves on the branch with a unique number using permanent marker, and each month we took a digital photograph of each leaf. Using the digital images we counted the number of fungal lesions and mines and calculated the exact percentages of leaf chewed. Herbivory area was calculated by placing a transparency with a 5mm grid over digital photos, counting total number of squares covered by the leaf and total number of squares of missing leaf. Percent was then calculated as missing leaf divided by missing + visible leaf. We here present data for three sample months – one near the start of the experimental period (August 2010), one near the middle (February 2010), and one near the end (May 2010). We examined all harvested fruits (see below) for attack by the coffee berry borer to determine the percentage of fruits attacked in each habitat.

Significant differences in leaf damage were assessed in two ways. First, we compared total standing leaf damage -- the mean number of lesions, mines, and percent herbivory -- across the three sample months and habitats using repeated measures ANOVA. We also calculated the accumulation of damage across the study period by subtracting the total amount of damage on individual leaves in August 2009 from damage recorded in May 2010. Differences in mean accumulation of fungal lesions, mines, and herbivory were compared with univariate ANOVA. We compared the mean proportion of fruits with the coffee berry borer using univariate ANOVA. We log (ln+1) transformed number of fungal lesions and mines and arcsin square root transformed proportion of leaf damage and fruits with borer to meet conditions of normality.

Coffee yields:
For each experimental plant, we used stratified random sampling to select six branches per plant: two in the top third of the plant, two in the middle third, and two in the lower third. We counted and harvested all coffee berries from each branch. Fruit numbers and weights were summed for the two plants in each group and then compared with univariate ANOVA. Data for fruit number and weights were log (ln+1) transformed to meet conditions of normality. After weighing, all coffee fruits were returned to the farm processing plant.

5. Project Results

Local environmental factors:
As expected, there were several significant differences in the vegetation characteristics of the cut and uncut areas (Table 1). Overall the vegetation differed in the three habitat types ($F_{12, 136}=10.294$, $P<0.001$). There were fewer trees in the area cut in 2008 than in the uncut area ($P=0.001$) or the area cut in 2007 ($P=0.02$). There were also fewer tree species in the most recently cut area compared with the uncut area ($P<0.001$) or the area cut in 2007 ($P=0.037$). The canopy of the most recently cut area was more dominated by trees in the genus *Inga* than the uncut habitat ($P=0.019$). Trees were smaller in the area cut in 2008 than in the uncut area in terms of circumference ($P=0.011$) and tree height ($P < 0.001$), and trees were shorter in the area cut in 2007 than in the uncut area ($P<0.001$). Finally canopy cover differed in each habitat with highest cover in the uncut area with 20% more cover than in the area cut in 2007 ($P<0.001$), and 3 times more cover than in the area cut in 2008 ($P<0.001$). Thus, overall, the vegetation was most complex in terms of richness and vertical structure in the uncut habitat and most simplified in the area cut in 2008 (Table 1).

Arthropods:
We collected a total of 9328 arthropods from 18 different orders during the four sample periods. The most abundant orders were Diptera (flies) with 4075 individuals, Hymenoptera (ants, bees, wasps) with 2181 individuals, and Hemiptera (plant hoppers, scale insects, leaf bugs) with 895 individuals. This total included 39 families of beetles, the most common were Chrysomelidae

(herbivorous leaf beetles) with 152 individuals, Staphylinidae (predatory rove beetles) with 57 individuals, and Ptiliidae (fungivorous featherwing beetles) with 41 individuals.

Although the abundance of some arthropods varied with date there were few overall differences in abundance of different feeding groups between habitat types (Fig. 4). There were no differences between habitats in terms of abundance of all arthropods ($F_{2,288}$=1.748, P=0.176), herbivores ($F_{2,288}$=0.116, P=0.890), beneficial arthropods ($F_{2,288}$=2.241, P=0.108), predators ($F_{2,288}$=2.058, P=0.13), decomposers ($F_{2,288}$=1.778, P=0.171), or for the herbivore:beneficial arthropod ratio ($F_{2,288}$=0.556, P=0.574). Likewise, there were few differences in the abundance of different arthropod taxa examined in the different habitat types (Fig. 5). There were no differences in abundance of spiders ($F_{2,288}$=2.135, P=0.120), beetles ($F_{2,288}$=2.373, P=0.095), caterpillars ($F_{2,288}$=1.558, P=0.212), or parasitoid wasps ($F_{2,288}$=0.477, P=0.621) aspirated with the D-VAC. In contrast, abundance of ants collected with the D-VAC differed by habitat type ($F_{2,288}$=5.831, P=0.003) with twice as many ants in the uncut area (P=0.007) and in the area cut in 2007 (P=0.012) than in the area cut in 2008. There were many differences in abundance of different feeding groups and taxa by date, and also significant interactions between date and habitat indicating that there was significant fluctuation in abundance over time, and that patterns differed with habitat type. However, because the intent was to primarily compare overall patterns across habitat types, these results are not discussed here. There was no significant correlation between the abundance of herbivores, beneficial arthropods or the herbivore: beneficial ratio and the canopy cover at the study plots.

Natural enemy surveys:
We collected a total of 47 species of ants in the three habitat types (Appendix 1). The abundance of ants was similar in the three habitat types with on average 11.72 ± 0.56 occurrences in the uncut area, 11.56 ± 0.51 occurrences in the area cut in 2007, and 11.4 ± 0.79 occurrences in the area cut in 2008 ($F_{2,72}$=0.064, P=0.937). The number of ant species found was significantly higher in the area cut in 2008 (36 species) than in the area cut in 2007 (27 species), but there were no differences in the number of ant species in the uncut area (35 species) and other habitats (Fig. 6a). The estimated number of ant species was higher in the uncut area and area cut in 2008 than the area cut in 2007 (Fig. 6b).

With visual searches we found a total of 2722 spiders during July and Oct 2009, and Feb and April 2010. Spider abundance differed with habitat type ($F_{2,72}$=3.714, P=0.029) (Fig. 5). Specifically, there were about half again as many spiders in the area cut in 2008 than in the area cut in 2007 (P<0.05) but no differences between abundance in the uncut area and the area cut in 2008 (P>0.05) or the area cut in 2007 (P>0.05).

Herbivore surveys:
There was no difference in the abundance of scale insects in different sites with nearly identical abundance ($F_{2,288}$=1.128, P=0.325) (Fig. 5). However, scale abundance did vary drastically over time with higher abundance in July 2009 than in any other month ($F_{3,288}$=12.213, P<0.001).

Plant damage:
Overall, coffee leaf damage was very limited in all habitats. On average, there were fewer than 0.5 ojo de gallo lesions, 0.3 leaf rust lesions, and 0.03 leaf mines per leaf, and less than 1.5% of leaf consumed by chewing herbivores (Fig. 7a-d). There were significant differences, nonetheless, in the amount of damage present and for damage accumulated in the different habitats for some types of

damage. Generally, there was more fungal damage and herbivory in the uncut areas than in cut areas but leaf miner damage did not differ.

Specifically, there were 2-3 times more ojo de gallo lesions in the uncut area than in at least one of the two cut habitats for all dates examined ($F_{2,72}$=3.69, P=0.03) (Fig. 7b). Uncut areas had more ojo de gallo than the area cut in 2007 in Aug. (P=0.028) and more than the area cut in 2008 in Feb. (P=0.031) and May (P=0.041). Four times more ojo de gallo was accumulated on leaves in the uncut area than in the area cut in 2007 (P=0.021) or 2008 (P=0.001) ($F_{2,72}$=7.502, P=0.001) (Fig. 8b). There was at least two times as much herbivory on coffee leaves in the uncut area than in the area cut in 2008 on all sample dates (Aug., P<0.001; Feb., P=0.01; May, P<0.001) with differences between the uncut area and the cut 2008 only for May (P<0.001) ($F_{2,72}$=15.208, P<0.001) (Fig. 7d). More herbivory accumulated in the uncut area than in the areas cut in 2007 (P=0.01) and 2008 (P=0.002) ($F_{2,72}$=7.219, P=0.001) (Fig. 8d). In contrast, there were no differences in the number of leaf rust lesions in the different habitats during Aug., Feb., and May samples ($F_{2,,72}$=1.492, P=0.232) (Fig. 7a). But leaves accumulated twice as much leaf rust in the uncut habitat than in the area cut in 2007 (P=0.05) or 2008 (P=0.03)($F_{2,72}$=4.28, P=0.02) (Fig. 8a). There were no differences in the number of leaf mines in different months or habitats ($F_{2,72}$=0.656, P=0.522) (Fig. 7c), and there was no difference in the amount of leaf miner damage accumulated ($F_{2,72}$=0.97, P=0.39) (Fig. 8c).

Coffee fruit damage was somewhat more substantial with between 2-12% of fruits lost to the coffee berry borer (Fig. 9c). There was a significantly higher fraction of fruits attacked by the coffee berry borer in the uncut area than in either of the two cut areas ($F_{2,70}$=10.806, P<0.001). There were four times more fruits in the uncut than in the area cut in 2007 (P=0.003) and six times more attacked fruits in the uncut than in the area cut in 2008 (P<0.001).

Coffee yields:
Coffee yields were higher in the two cut areas compared with the uncut habitat (Fig. 9a,b) in terms of total number of undamaged fruits produced ($F_{2,70}$=12.596, P<0.001) and in terms of total fruit weight ($F_{2,70}$=7.837, P=0.001). The number of undamaged fruits was nearly three times higher in the area cut in 2007 than in the uncut area (P<0.001) and 2.5 times greater in the area cut in 2008 than in the uncut area (P<0.001). Similarly, fruit weights were more than twice as high in the area cut in 2007 than in the uncut (P=0.001), and 1.5 times higher in the area cut in 2008 than in the uncut (P=0.015).

6. Conclusions and Discussion

Several measured factors differed with shade management type. We found significant differences in vegetation, not surprisingly, with more trees, more tree species, larger and taller trees, and more canopy cover in the uncut area compared with the cut areas. Thus, vegetation complexity was reduced by the shift in the shade management regime. The shift in the shade did not have large effects on arthropods overall, but arthropods were abundant and diverse in the farm. We found no change in abundance of herbivores, predators, decomposers, beneficial arthropods, the ratio of herbivores to beneficial arthropods, spiders, beetles, parasitoid wasps, or caterpillars in the three habitat types. There were, however, several seasonal changes in arthropod abundance and a few differences between sites during certain months. More specific surveys of two natural enemies (ants and spiders) did reveal some differences. There were more ant species in the area cut in 2008 and in the uncut area compared with the area cut in 2007. Ant abundance was greater in the uncut area and the area cut in 2007, and spider abundance was higher in the area cut in 2007 than in the area cut in

2008. Thus, specific taxa of natural enemies appeared to be either more diverse or more abundant in less disturbed habitats. There were larger differences in plant damage and yield between habitats. There was more fungal disease caused by ojo de gallo in the uncut habitat, and more herbivory. Further, there was more accumulation of fungal diseases (ojo de gallo and leaf rust) in the uncut area and twice as much herbivory accumulation. There was more damage caused by the coffee berry borer, with twice as much damage in uncut areas. Finally, coffee yields were twice as high in the cut areas, both in terms of total fruits produced and fruit weight. Thus, in this study, we documented both higher presence of natural enemies and higher damage in the uncut habitats and higher yields in the cut habitats.

Several aspects of this study deserve further discussion and attention. Even though abundance and richness of some natural enemies was higher in the uncut area, the damage sustained by leaves and fruits was still higher in the uncut areas. The two natural enemy groups examined are important predators of coffee pests. Several species of ants, in particular, attack the coffee berry borer (Velez *et al.* 2003, Perfecto & Vandermeer 2006, Armbrecht & Gallego 2007). The abundance of those two groups was higher in the specific surveys aimed at finding ants (with baits) and spiders (with visual searches), leading to this somewhat counterintuitive result. However there are many other predators that occur naturally in coffee farms and their abundance may also have been strongly affected by the shade cutting. For example, in another study in the same sites following the shade tree cutting, we documented that abundance, species richness, and functional group richness of insectivorous birds dropped by half in cut habitats (Philpott & Bichier, in review). Such insectivores also prey on the coffee berry borer (Kellermann et al. 2008) and the leaf miner (Borkhataria *et al.* 2006). Further, other insectivores such as bats and lizards that also prey on coffee pests may have been affected but were not studied. In a nutshell, coffee agroecosystems are extremely complex systems (Vandermeer *et al.* 2010), and any changes in one group of organisms may cascade to another group with sometimes unanticipated effects.

Further, the levels of herbivory and other leaf damage were significantly different, as were yields. However, it is important to question whether these significant but small differences in coffee leaf damage would actually affect coffee yield. The amounts of herbivory were under 2% leaf consumed on average, and fungal disease lesions were fewer than one per leaf. Several other factors certainly affect coffee yields in a much more dramatic way including rainfall, light availability, photosynthetic rate, and soil nutrients (Magalhaes and Angelocci 1976, Cannell 1983, Carr 2001, Lin *et al.* 2008).

Specifically, because so many factors affect coffee yields, including soil conditions, elevation, precipitation, inputs, coffee variety, and shade, it has been very difficult to make clear statements about the relationship between shade, *per se*, and yield or even to compare across studies with more quantitative methods (e.g. meta-analysis) (Perfecto *et al.* 2005). In fact, the uncut traditional polyculture in this farm is not actively managed in any way, with little to no trimming of the shade trees, no application of compost or other organic matter, and no regular removal of dead branches on the coffee plants themselves. In contrast, in the cut areas of the farms, most plants receive compost tea or compost at least one a year, providing the plants with needed nutrients for production. Thus, the uncut area is nearly abandoned. Often, the fruits are not harvested; many of the fruits drop to the ground where they make perfect breeding grounds for the coffee berry borer from season to season (Larsen & Philpott 2010). Thus, even though increases in plant damage may have resulted in lower yields in the uncut habitat in this case, it is likely that other factors, such as a lack of organic soil inputs, may have had greater influences on overall yields. The uncut traditional polyculture on this farm was the only available control for the cut habitats – as it remained the only uncut area of the farm. However, it did not make an ideal control for only examining the impact of the shade management change due to other differences (e.g. compost application, harvesting) between the cut and uncut areas.

One of the most interesting aspects of the study is that it does provide some evidence that there is a trade-off between biodiversity and yields in coffee agroecosystems. Several studies have examined biodiversity of ants, birds, bees, butterflies, and other taxa in these same farms, with the vast majority finding higher richness in the uncut traditional polyculture compared with the commercial polyculture areas. However, the study presented here documents clearly that there is higher plant damage and less yield in the uncut area. This may be due to shade management alone (and related factors such as light availability), however, soil management may also be a factor. Thus, if farmers are truly interested in promoting biodiversity-friendly coffee, their yields may decline to some extent. Thus consumers and certification groups should work towards figuring out ways to best compensate farmers for any reduced yields and farmers must look towards examining strategies to increase yields in shaded farms. Investigating the impacts of composting in shaded and unshaded farms could be an interesting direction for future research in organic coffee farms.

7. Outreach

To date, little outreach has been carried out specific to this research, as the findings have just been analyzed. We do plan to share this report with the farmers participating in the study and with farm workers and farmer organizations. To make the findings available to farmers and to farmer organizations, we will produce a user-friendly pamphlet in Spanish to summarize effects of shade tree cutting and removal on arthropods, plant damage, and on coffee yields. We will outline the specific methods in layman's terms and will use drawings and graphs to explain the results. At a local level in Chiapas, we will distribute the pamphlet directly to farmers in the watershed where the research will be conducted and will make use of the extensive outreach network of El Colegio de la Frontera Sur (ECOSUR) for disseminating the pamphlet to other producers in the Soconusco. We will also distribute the information to smallholder cooperatives in the Chiapas and Oaxaca highlands that are connected through a series of umbrella organizations (e.g. Café Museo, MasCafe, Comercio Justo Mexico). We will work in conjunction with scientists and outreach educators from the Smithsonian Migratory Bird Center to distribute the pamphlet to a wider audience of Bird-Friendly certified shade coffee producers.

To make our findings available to workers in the coffee region, we will present workshops, aimed towards an audience of school children living in the farm. There are approximately 30 families that live at Finca Irlanda, many of which have lived on the farm for their entire lives. We will prepare a series of general talks to discuss biodiversity, arthropod biology, biological control, water protection, and ecology of pest problems to provide general science education to the community at the farm.

We have one manuscript in review (at Agriculture, Ecosystems, and Environment) relating to the impact of shade tree cutting on bird communities that was partly sponsored by the OFRF grant, and we plan to submit at least 1-2 more manuscripts of the findings to the scientific literature (e.g. *Ecological Applications*, *Conservation Biology*, *Biological Control*, *Environmental Entomology*). The results have been presented at local symposia (U. of Toledo and U. of Michigan) and we plan to make presentations at ECOSUR and at international conferences (e.g. Ecological Society of America, Association for Tropical Biology and Conservation) in the coming year.

8. References

Agne, S. 2000. The impact of pesticide taxation on pesticide use and income in Costa Rica's coffee production. MS Thesis, Hanover University.

Armbrecht, I., and M. C. Gallego. 2007. Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. Entomologia Experimentalis et Applicata **124**:261-267.

Armbrecht, I., L. Rivera, and I. Perfecto. 2005. Reduced diversity and complexity in the leaf litter ant assemblage of Colombian coffee plantations. Conservation Biology **19**:897-907.

Beer, J. 1987. Advantages, disadvantages, and desirable characteristics of shade trees for coffee, cacao, and tea. Agroforestry Systems **5**:3-13.

Borkhataria, R. R., J. A. Collazo, and M. J. Groom. 2006. Additive effects of vertebrate predators on insects in a Puerto Rican coffee plantation. Ecological Applications **16**:696-703.

Cannell, M. 1983. Coffee. Biologist **30**:257-263.

Carr, M. 2001. The water relations and irrigation requirements of coffee. Experimental Agriculture **37**:1-36.

Chesson, P. L., and T. J. Case. 1986. Overview: Nonequilibruim community theories: Chance, variability, history, and coexistence. Pages 229-239 *in* J. Diamond and T. J. Case, editors. Community Ecology. Harper and Row, New York.

Coyner, M. S. 1960. Agriculture and trade in Nicaragua. Foreign Agricultural Service, Washington DC.

De Graaf, R. 1986. The economics of coffee. Publikatiene Documentatie Dienst Landbouw Onderzoek, Wageningen.

De la Mora, A., G. Livingston, and S. M. Philpott. 2008. Arboreal Ant Abundance and Leaf Miner Damage in Coffee Agroecosystems in Mexico. Biotropica **40**:742-746.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Chapman and Hall, London, England.

Flynn, D. F. B., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. Trautman Richers, B. B. Lin, N. Simpson, M. M. Mayfield, and F. DeClerck. in press. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters.

Greenberg, R., B. Bichier, A. Cruz Angon, C. MacVean, R. Perez, and E. Cano. 2000. The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. Ecology **81**:1750-1755.

Ibarra-Núñez, G. 1990. Los artrópodos asociados a cafetos en un cafetal mixto del Soconusco, Chiapas. México: I Variedad y Abundancia. Folia Entomológica Mexicana **79**:207-231.

Ives, A. R., B. J. Cardinale, and W. E. Snyder. 2005. A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. Ecology Letters **8**:102-116.

Kellermann, J. L., M. D. Johnson, A. M. Stercho, and S. C. Hackett. 2008. Ecological and economic services provided by birds on Jamaican Blue Mountain coffee farms. Conservation Biology 22:1177–1185.

Larsen, A., and S. M. Philpott. 2010. Twig-nesting ants: The Hidden predators of the coffee berry borer in Chiapas, Mexico. Biotropica **42**:342-347.

Le-Pelley, R. 1973. Coffee insects. Annual Review of Entomology **18**:121-142.

Letourneau, D. K., and S. G. Bothwell. 2008. Comparison of organic and conventional farms: challenging ecologists to make biodiversity functional. Frontiers in Ecology and Environment **6**:430-438.

Lin B. B., I. Perfecto, and J. Vandermeer. 2008. Synergies between Agricultural Intensification and Climate Change Could Create Surprising Vulnerabilities for Crops. Bioscience **58**:847-854.

Lomeli Flores, J. R. 2007. Natural enemies and mortality factors of the coffee leaf miner *Leucoptera coffeella* (Guerin-Meneville) (Lepidoptera: Lyonetiidae) in Chiapas, Mexico. Texas A&M University.

Losey, J. E., and R. F. Denno. 1999. Factors facilitating synergistic predation: the central role of synchrony. Ecological Applications **9**:378-386.

Magalhaes, A., and L. Angelocci. 1976. Sudden alterations in water balance associated with flower bud opening in coffee plants. Journal of Horticultural Science **51**:419-421.

Perfecto, I., I. Armbrecht, Philpott S.M., Soto-Pinto L, and D. TV. 2007. Shaded coffee and the stability of rainforest margins in Latin America. Pages 227-263 *in* T. Tscharntke, C. Leuschner, M. Zeller, E. Guhadja, and A. Bidin, editors. The stability of tropical rainforest margins, linking ecological, economic and social constraints of land use and conservation. Springer, Environmental Science Series, Heidelberg and New York.

Perfecto, I., R. A. Rice, R. Greenberg, and M. E. VanderVoort. 1996. Shade coffee: A disappearing refuge for biodiversity. Bioscience **46**:598-608.

Perfecto, I., and J. Vandermeer. 1996. Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. Oecologia **108**:577-582.

Perfecto, I., and J. Vandermeer. 2002. Quality of agroecological matrix in a tropical montane landscape: Ants in coffee plantations in southern Mexico. Conservation Biology **16**:174-182.

Perfecto, I., and J. Vandermeer. 2006. The effect of an ant-hemipteran mutualism on the coffee berry borer (*Hypothenemus hampei*) in southern Mexico. Agriculture, Ecosystems & Environment **117**:218-221.

Perfecto, I., J. Vandermeer, P. Hanson, and V. Cartin. 1997. Arthropod biodiversity loss and the transformation of a tropical agro-ecosystem. Biodiversity and Conservation **6**:935-945.

Perfecto, I., J. Vandermeer, A. Mas, and L. Soto-Pinto. 2005. Biodiversity, yield, and shade coffee certification. Ecological Economics **54**:435-446.

Philpott, S. M., W. Arendt, I. Armbrecht, P. Bichier, T. Dietsch, C. Gordon, R. Greenberg, I. Perfecto, L. Soto-Pinto, C. Tejeda-Cruz, G. Williams, and J. Valenzuela. 2008a. Biodiversity loss in Latin American coffee landscapes: reviewing evidence on ants, birds, and trees. Conservation Biology **22**:1093-1105.

Philpott, S. M., and I. Armbrecht. 2006. Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. Ecological Entomology **31**:369-377.

Philpott, S. M., and P. Bichier. *in review*. Effects of shade tree removal on birds in coffee agroecosystems in Chiapas, Mexico. Agriculture, Ecosystems, and Environment.

Philpott, S. M., I. Perfecto, and J. Vandermeer. 2008b. Behavioral diversity of predatory ants in coffee agroecosystems. Environmental Entomology **37**:181-191.

Pimentel, D. A., U. Stachow, D. A. Takacs, H. W. Brubaker, A. R. Dumas, J. J. Meaney, J. A. O'Neil, D. E. Onsi, and D. B. Corzilius. 1992. Conserving biological diversity in agricultural/forestry systems. Bioscience **42**:354-362.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs **43**:95-124.

Schulze, E. D., and H. A. Mooney. 1993. Biodiversity and Ecosystem Function. Springer-Verlag, Berlin.

Soto-Pinto, L., I. Perfecto, J. Castillo-Hernandez, and J. Caballero-Nieto. 2000. Shade effect on coffee production at the northern Tzeltal zone of the state of Chiapas, Mexico. Agriculture Ecosystems & Environment **80**:61-69.

Van Bael, S. A., S. M. Philpott, R. Greenberg, P. Bichier, N. A. Barber, K. A. Mooney, and D. S. Gruner. 2008. Birds as predators in tropical agroforestry systems. Ecology **89**:928-934.

Vandermeer J., I. Perfecto, and S. M. Philpott. 2010. Ecological complexity and pest control in organic coffee production: Uncovering an autonomous ecosystem service. Bioscience **60**: 516-526

Vélez, M., A. E. Bustillo, and F. Posada. 2003. Depredación de *Hypothenemus hampei* por *Solenopsis* *geminata* y *Gnamptogenys* sp. (Hymenoptera: Formicidae). Page 26 *in* Libro de Resumenes XXX Congreso, Sociedad Colombiana de Entomología, Cali, Universidad Autonoma.

Western, D., and M. C. Pearl. 1989. Conservation for the twenty-first century. Oxford University Press, New York.

Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proceedings of the National Academy of Sciences of the United States of America **96**:1463-1468.

9. Acknowledgments

This work would not have been possible without the cooperation of Don Walter Peters and Bernd Peters, owners of Finca Irlanda. We also thank Gabriel Dominguez Martinez, Cody Murnen, Leigh Moorhead, Jenna Svenson, Gustavo Lopez Bautista, Braulio Esteben Chilel, and Aldo De la Mora who helped with data collection, identification, and leaf analysis.

10. Tables, Figures, and Appendix

Table 1. Vegetation characteristics of three habitat types in an organic coffee agroecosystem in Chiapas, Mexico.

Vegetation Variable	Uncut[†]	Cut in 2007	Cut in 2008	$F_{2, 72}$	P
No. of tree individuals	10.52 ± 1.04a	9.16 ± 0.5a	7.2 ± 0.67b	7.33	0.001
No. of tree species	6.32 ± 0.44a	5.28 ± 0.36a	3.96 ± 0.31b	10.18	<0.001
No. of *Inga* spp. individuals	2.8 ± 0.24b	3.76 ± 0.35a,b	4.2 ± 0.41b	4.07	0.021
Tree circumference (m)	71.56 ± 3.02a	63.06 ± 2.68a,b	60.34 ± 2.23b	4.84	0.011
Mean tree height (m)	10.96 ± 0.65a	6.7 ± 0.3b	6.31 ± 0.25b	34.86	<0.001
Canopy cover	89.85 ± 2.08a	66.23 ± 4.49b	28.08 ± 4.41c	66.31	<0.001

[†] Values show mean ± standard error.

Figure 1. Photos of the area cut in 2007 (a) and the uncut area (b) taken in 2007.

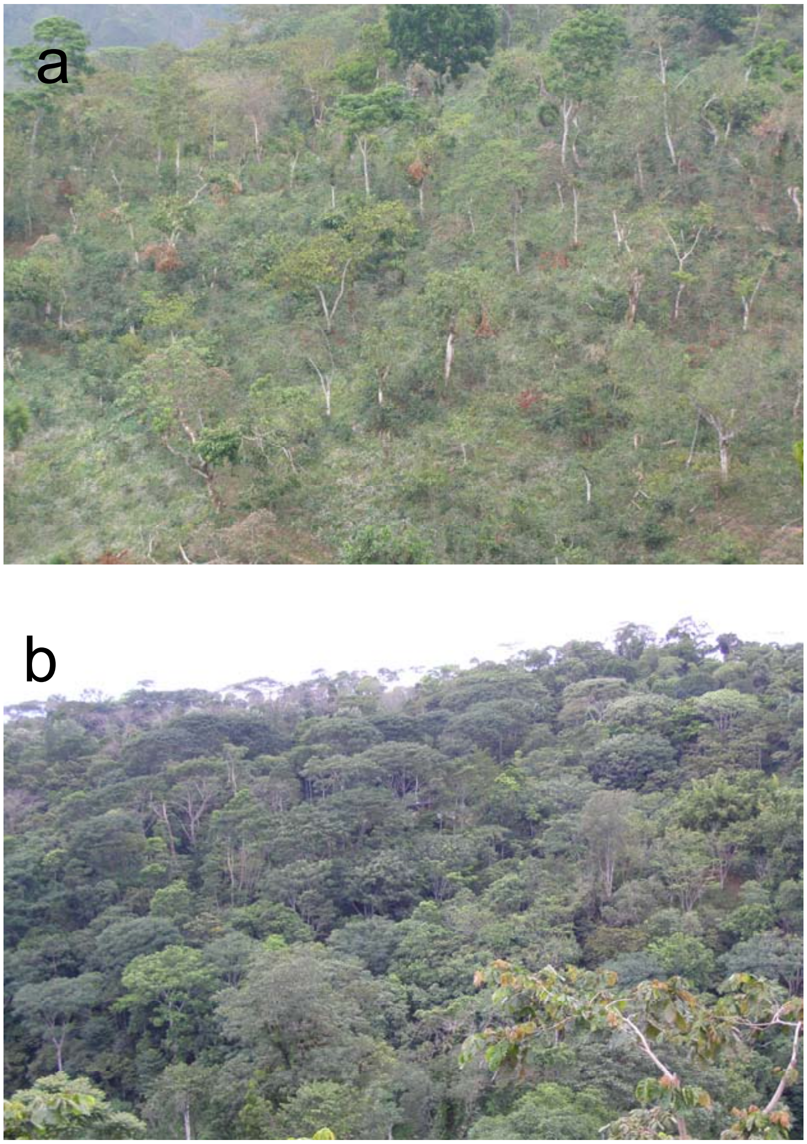


Figure 2. Map of the study plots in Finca Irlanda, an organic coffee farm in the Soconusco region of Chiapas, Mexico. In the map, R1-50 indicate marked plants in the uncut traditional polyculture habitat, B1-50 indicate marked coffee plants in the commercial polyculture area cut in May 2007, and A1-50 indicate plants in the commercial polyculture area cut in May 2008.

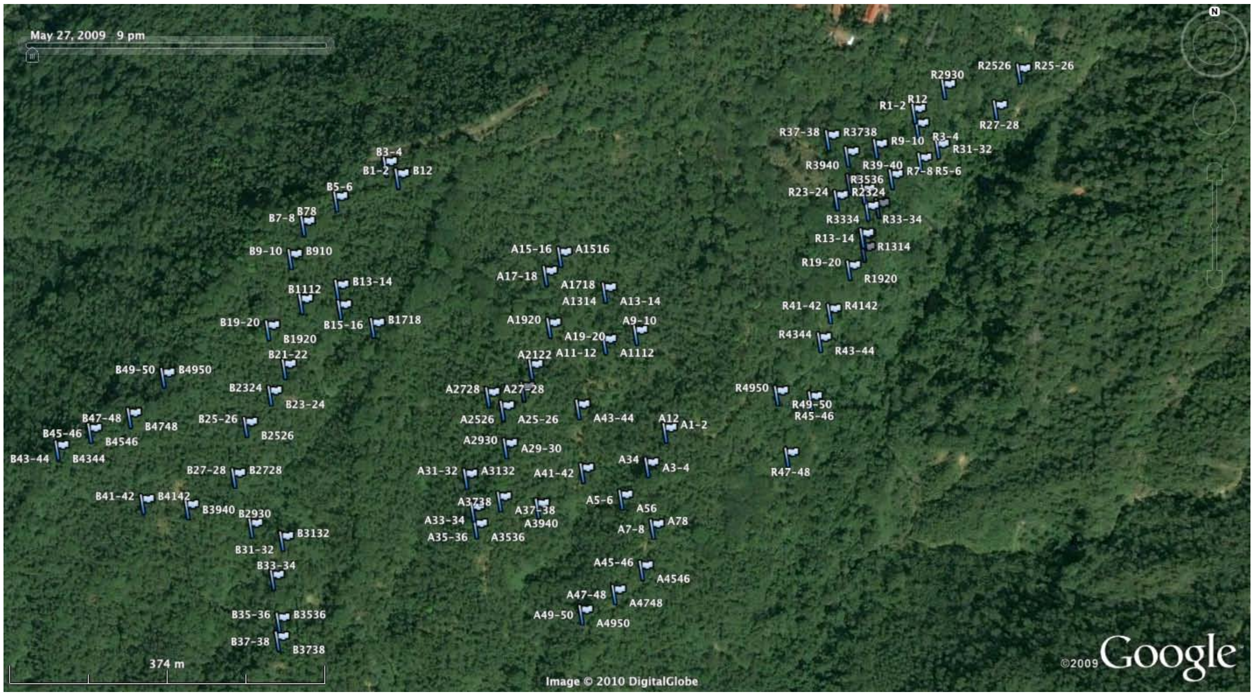


Figure 3. Images of types of leaf damage recorded in coffee farms. For all leaves photographed and examined, we measured the number of lesions of a) the coffee leaf rust (*Hemileia vastatrix*) and b) "ojo de gallo" (*Mycena citricolor*), c) the number of leaf mines created by the coffee leaf miner (*Leucoptera coffeella*), d) fraction of leaf consumed by chewing herbivores, e) number of scale insects per branch (*Coccus viridis*), and f) a coffee fruit attacked by the coffee berry borer (*Hypothenemus hampei*).

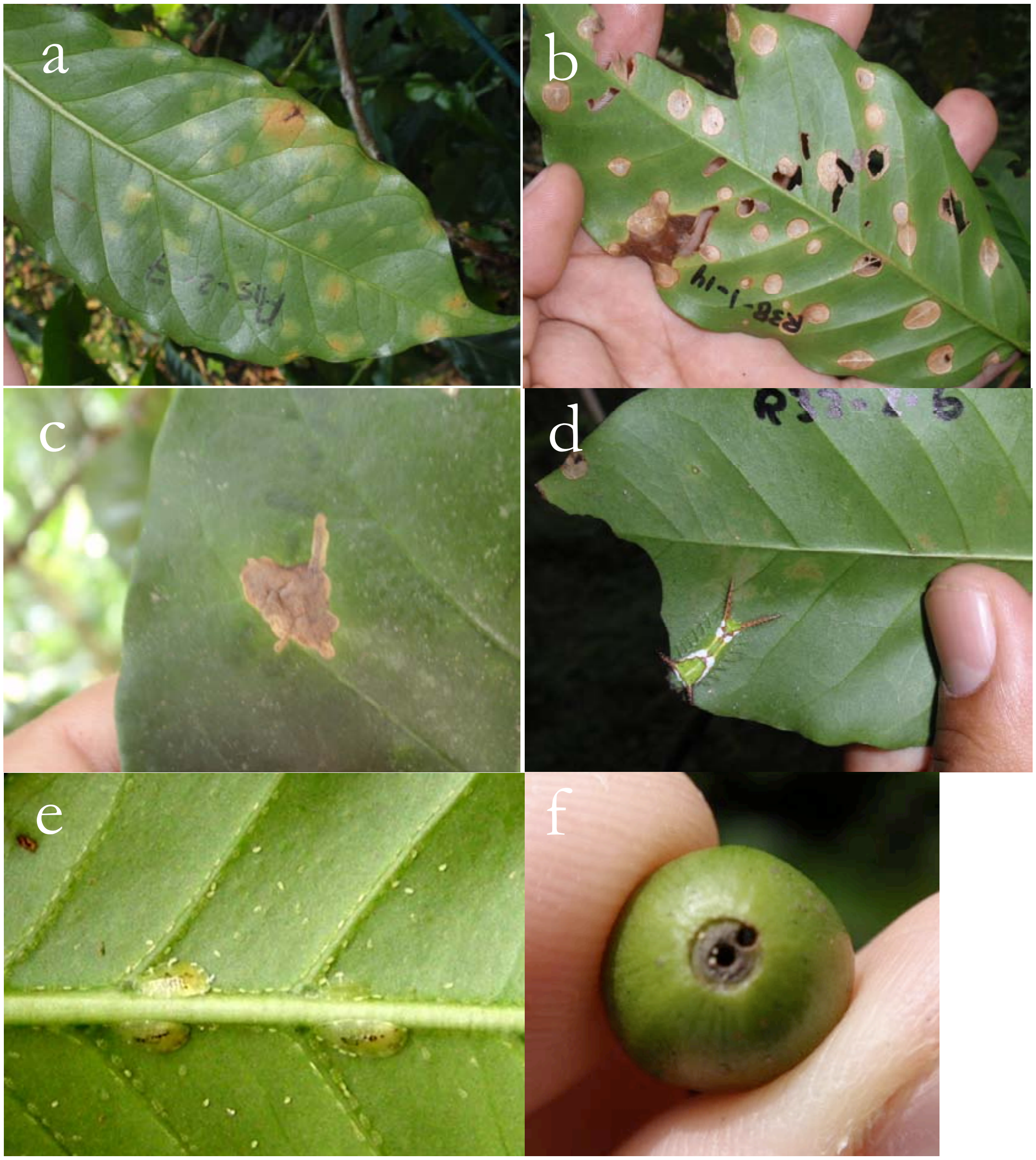


Figure 4. Arthropod abundance for total abundance and for feeding groups in the uncut area, the area cut in 2007, and the area cut in 2008. Graphs show mean ± standard error and n.s. indicates no significant differences in abundance between habitats. See text for explanation of differences.

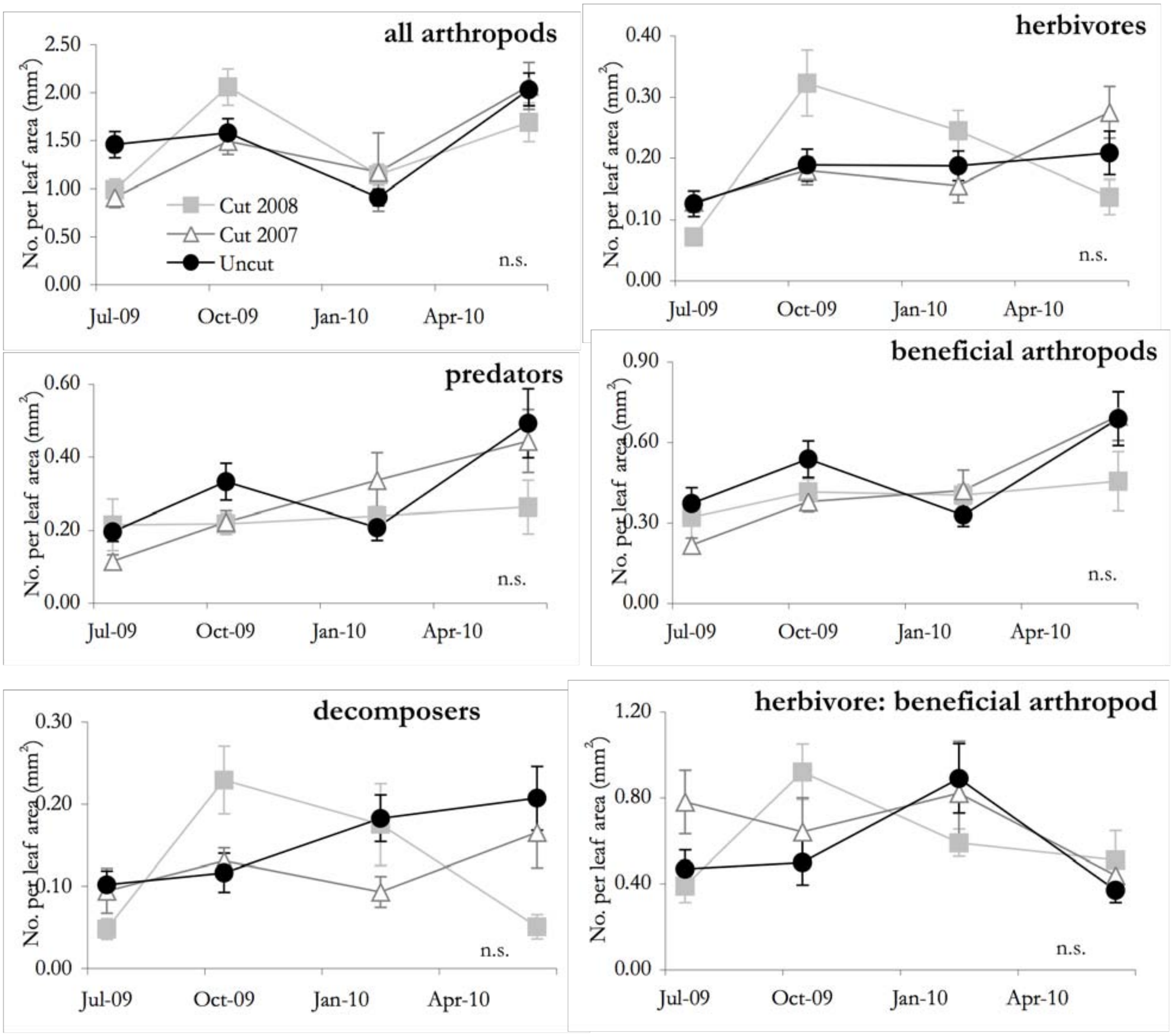


Figure 5. Arthropod abundance for different taxa in the uncut area, the area cut in 2007, and the area cut in 2008. Graphs show mean ± standard error and n.s. indicates no significant differences in abundance between habitats. See text for explanation of differences.

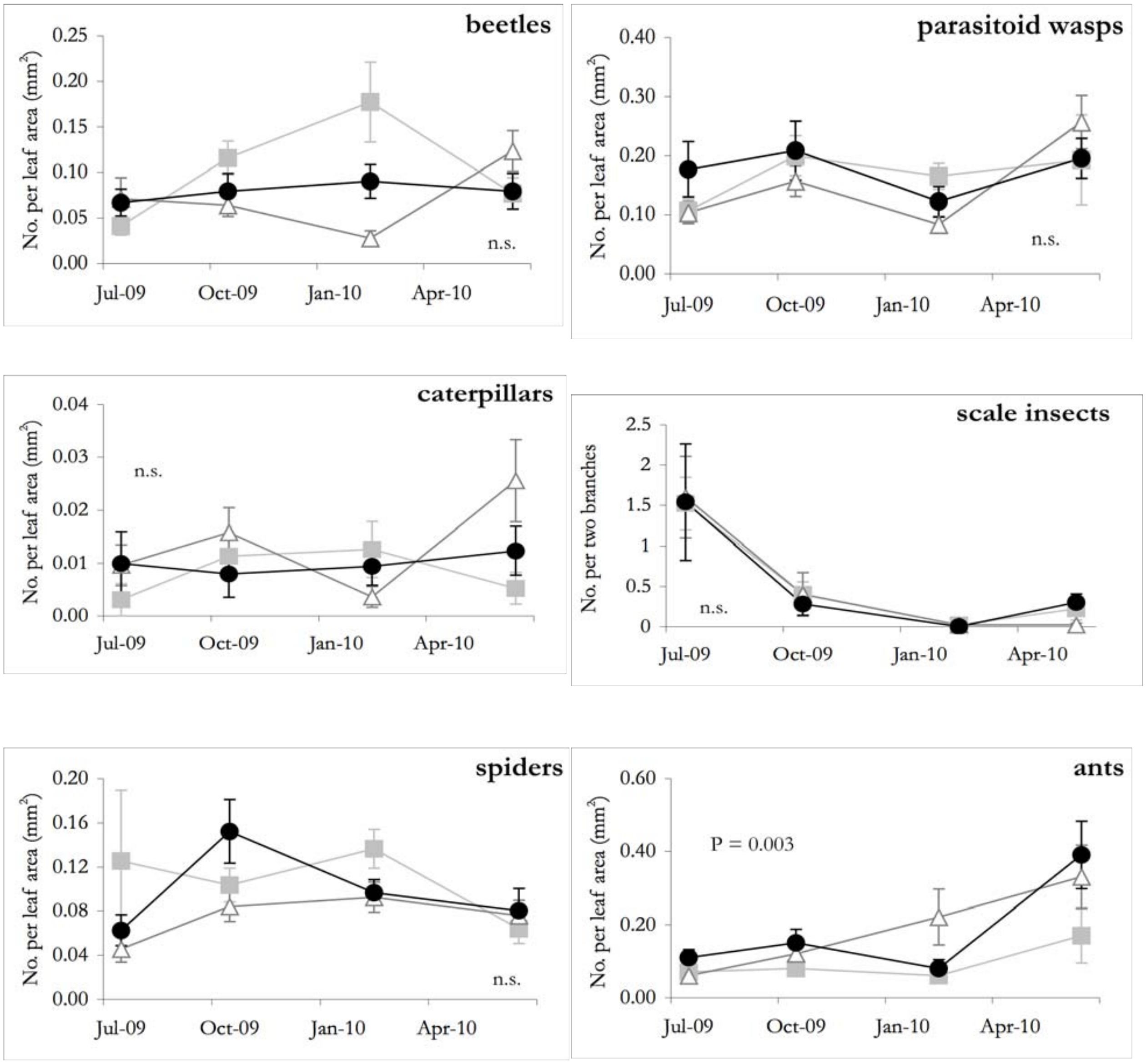


Figure 6. Ant species richness in the three coffee management areas; Uncut = traditional polyculture, Cut 2007 = commercial polyculture cut in 2007, Cut 2008 = commercial polyculture cut in 2008. Graphs show observed (a) and estimated (b) species richness, and error bars show 95% confidence intervals.

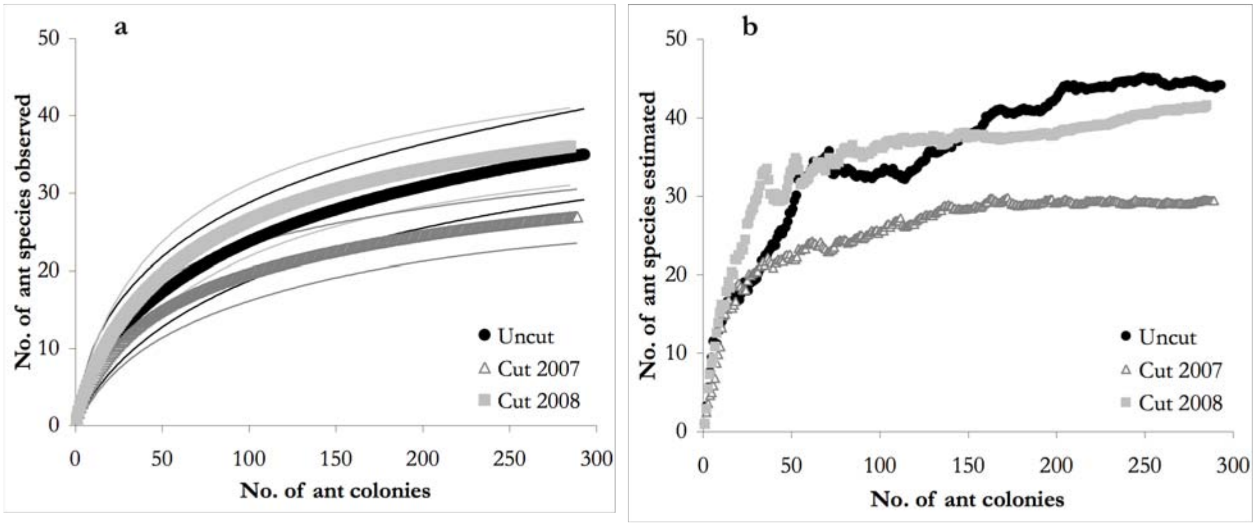


Figure 7. Leaf damage measured on plants in the uncut traditional polyculture, the commercial polyculture cut in 2007, and the commercial polyculture cut in 2008 in August 2009, February 2010, and May 2010. Graphs show mean values measured across 25 pairs of plants in each site for a) the coffee leaf rust (*Hemileia vastatrix*), b) ojo de gallo (*Mycena citricolor*), c) the number of leaf mines created by the coffee leaf miner (*Leucoptera coffeella*), and d) fraction of leaf consumed by chewing herbivores. Small letters next to symbols show significant differences in damage between habitats, n.s. is where no significant differences between treatments were found, and error bars show standard error.

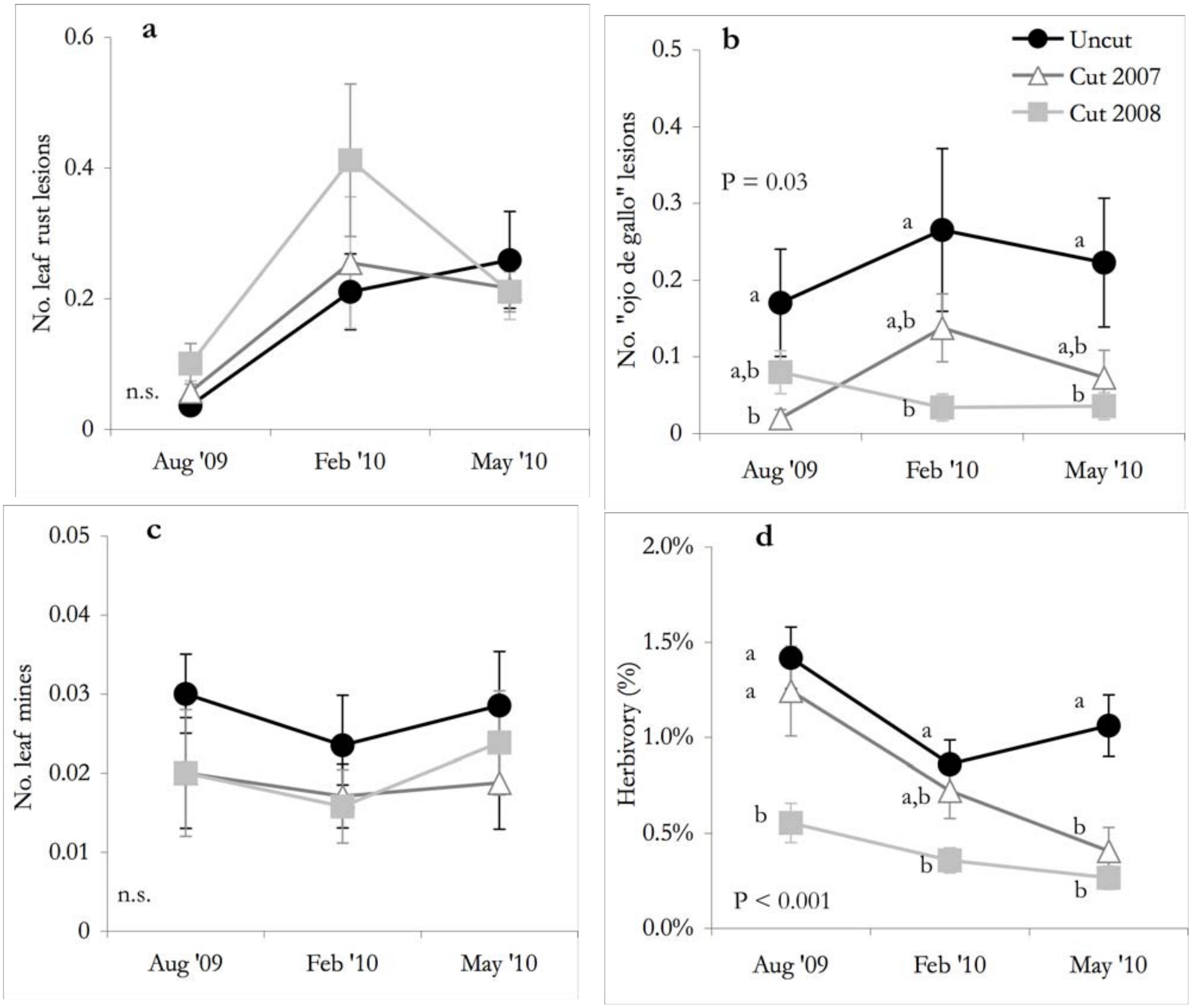


Figure 8. Amounts of damage accumulated on coffee leaves in the uncut traditional polyculture, the commercial polyculture cut in 2007, and the commercial polyculture cut in 2008 between August 2009 and May 2010. Values show the mean number of additional lesions per leaf of a) the coffee leaf rust (*Hemileia vastatrix*) or b) "ojo de gallo" (*Mycena citricolor*), c) the number of additional leaf mines per leaf created by the coffee leaf miner (*Leucoptera coffeella*), or d) increased percent of leaf consumed by chewing herbivores. Small letters next to symbols show significant differences in damage between habitats, n.s. is where no significant differences between treatments were found, and error bars show standard error.

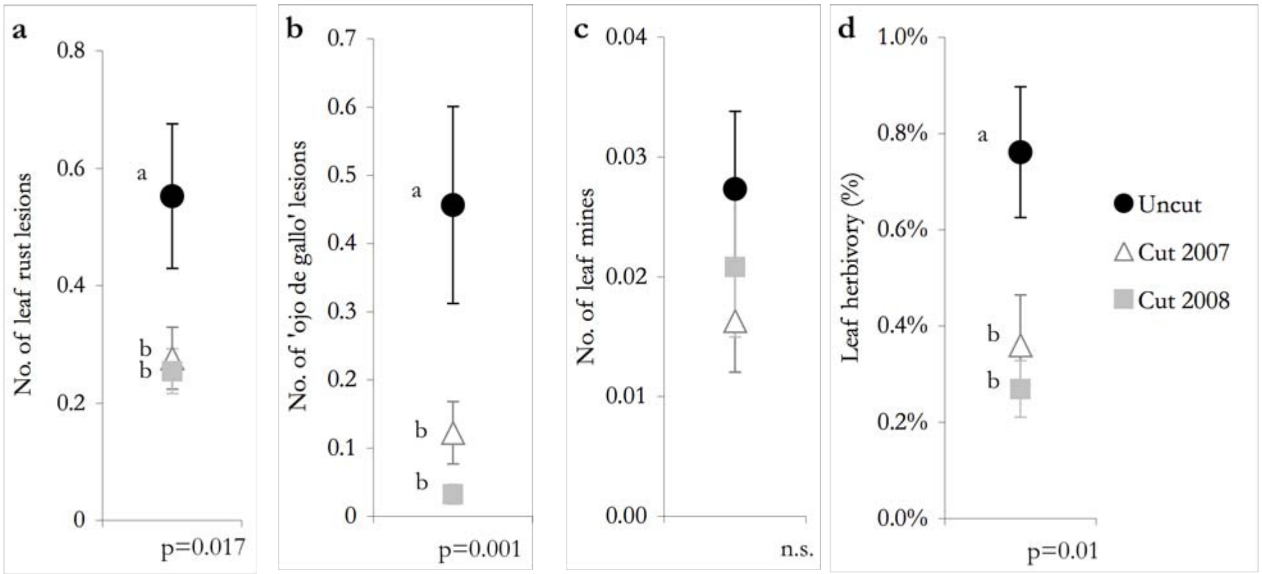
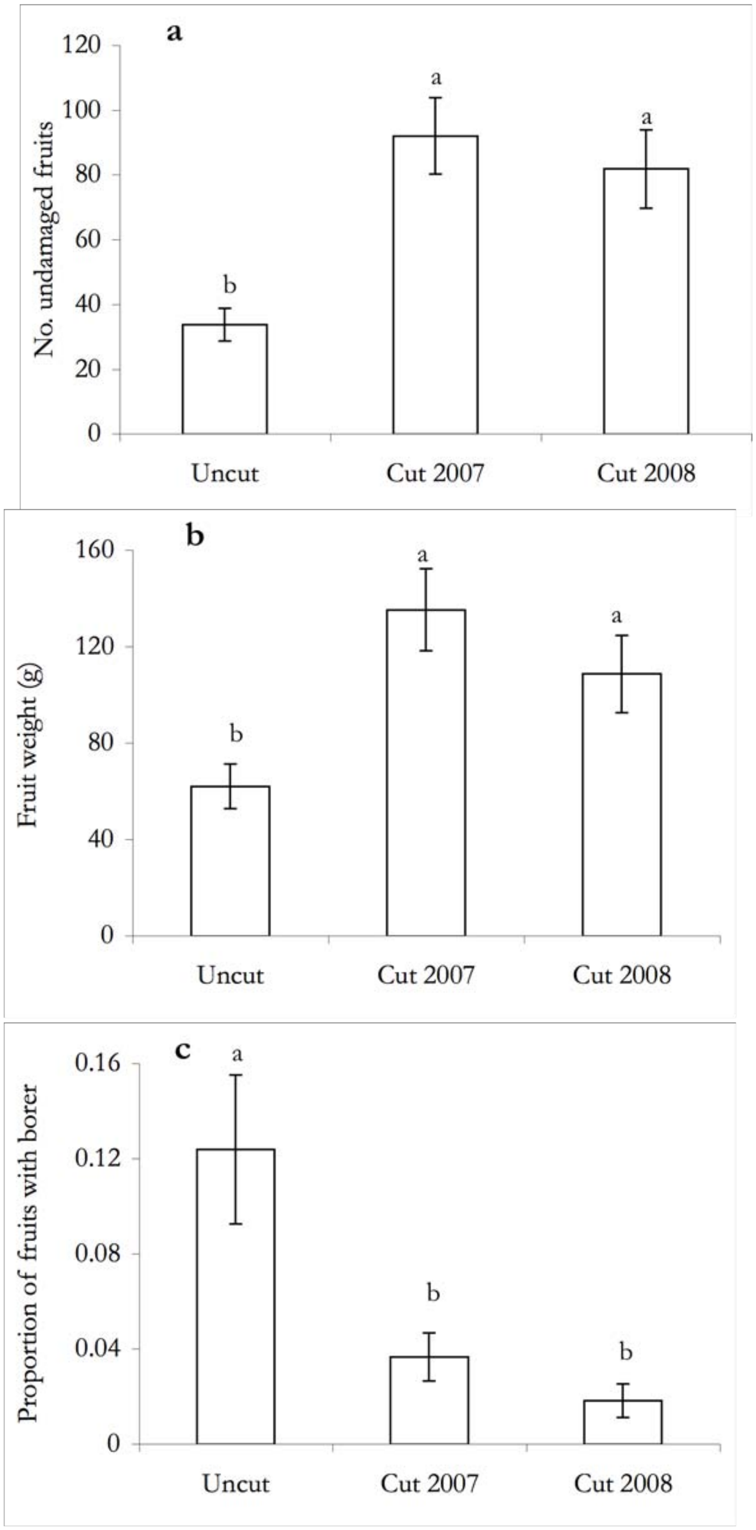


Figure 9. Mean coffee yield for two coffee plants measured as undamaged fruits (a) and total fruit weight (b), and proportion of fruits attacked by the coffee berry borer (c) for uncut traditional polyculture and two commercial polycultures cut during different years. Small letters show significant differences between habitats.



Appendix 1. List of ant species found in the three study areas.

Ant species	**Uncut**	**Cut 2007**	**Cut 2008**
Azteca instabilis	x		x
Brachymyrmex sp. 1	x	x	x
Brachymyrmex sp. 2	x	x	x
Camponotus bretessi	x		x
Camponotus novogranadensis	x	x	x
Camponotus senex			x
Camponotus sericeiventris		x	
Camponotus striatus	x	x	x
Camponotus textor	x	x	x
Camponotus (Colobopsis) sp. 1	x		
Cephalotes basalis	x	x	x
Crematogaster carinata	x	x	x
Crematogaster crinosa	x	x	x
Crematogaster nigropilosa	x	x	x
Crematogaster sumichrasti	x	x	x
Dolichoderus debilis	x		x
Eciton mexicanum		x	
Gnamptogeys sulcata			x
Leptogenys sp. 1	x		
Myrmelachista mexicana	x		
Myrmelachista sp. 1			x
Myrmelachista sp. 2		x	
Nesomyrmex echinatinodis	x	x	x
Nesomyrmex pittieri	x		
Paratrechina sp. 1	x		
Pheidole synanthropica	x	x	x
Pheidole indistincta	x	x	x
Pheidole protensa	x	x	x
Pheidole punctatissima	x	x	
Pheidole sp. 1	x		x
Pheidole sp. 2	x		x
Pheidole sp. 3			x
Plathythyrea punctata	x		
Procryptocerus hylaeus	x	x	x
Pseudomyrmex boopis			x
Pseudomyrmex ejectus		x	x
Pseudomyrmex elongatus			x
Pseudomyrmex gracilis	x	x	x
Pseudomyrmex PSW-53	x		x
Pseudomyrmex simplex	x	x	x
Solenopsis geminata			x
Solenopsis picea	x	x	x
Solenopsis terricola	x	x	
Solenopsis zeteki		x	x
Technomyrmex albipes	x	x	x
Technomyrmex fulvus	x	x	x
Wasmannia auropunctata	x		x
Total number of species	**35**	**27**	**36**