



Arboreal Ant Abundance and Leaf Miner Damage in Coffee Agroecosystems in Mexico

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ABSTRACT

Shaded coffee agroecosystems traditionally have few pest problems potentially due to higher abundance and diversity of predators of herbivores. However, with coffee intensification (*e.g.*, shade tree removal or pruning), some pest problems increase. For example, coffee leaf miner outbreaks have been linked to more intensive management and increased use of agrochemicals. Parasitic wasps control the coffee leaf miner, but few studies have examined the role of predators, such as ants, that are abundant and diverse in coffee plantations. Here, we examine linkages between arboreal ant communities and coffee leaf miner incidence in a coffee plantation in Mexico. We examined relationships between incidence and severity of leaf miner attack and: (1) variation in canopy cover, tree density, tree diversity, and relative abundance of *Inga* spp. shade trees; (2) presence of *Azteca instabilis*, an arboreal canopy dominant ant; and (3) the number of arboreal twig-nesting ant species and nests in coffee plants. Differences in vegetation characteristics in study plots did not correlate with leaf miner damage perhaps because environmental factors act on pest populations at a larger spatial scale. Further, presence of *A. instabilis* did not influence presence or severity of leaf miner damage. The proportion of leaves with leaf miner damage was significantly lower where abundance of twig-nesting ants was higher but not where twig-nesting ant richness was higher. These results indicate that abundance of twig-nesting ants in shaded coffee plantations may contribute to maintenance of low leaf miner populations and that ants provide important ecosystem services in coffee agroecosystems.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: agroforestry; *Azteca instabilis*; biodiversity and ecosystem service; biological control; Chiapas; *Leucoptera coffeella*; twig-nesting ant species.

THERE ARE OVER 900 HERBIVORES KNOWN TO FEED ON COFFEE (*Coffea arabica* L. (Rubiaceae)) (Kimani *et al.* 2002), but in traditional, shaded plantations, coffee has few pests (Odour & Simmons 2003). One hypothesis proposed to explain the relatively low levels of pest diversity and abundance in shaded coffee plantations is the increased diversity and abundance of predatory birds, bats, and arthropods in these habitats (Ibarra-Núñez 1990, Perfecto *et al.* 2004). Reductions in canopy cover and tree diversity in coffee plantations are associated with both losses of predator abundance and diversity (Philpott *et al.* in press) and increases in the incidence of pests. For example, the coffee leaf miner (*Leucoptera coffeella* Guerin-Meneville [Lepidoptera: Lyonetiidae]) is a coffee pest associated with management practices such as shade reduction and increased use of pesticides that accompany coffee intensification (Guharay *et al.* 2001, Fragoso *et al.* 2002, Carvalho *et al.* 2002, Lomeli Flores 2007). The coffee leaf miner causes extreme damage in coffee-producing areas dominated by plantations with limited shade in Brazil and Puerto Rico, where the proportion of damaged leaves normally reaches 20–40 percent, and the reduction in yields due to reduced photosynthesis can reach 40 percent (Martins *et al.* 2004, Bokhartaria *et al.* 2006,

Pereira *et al.* 2007). Leaf miner damage in southern Mexican can reach up to 12 percent, and the coffee leaf miner is considered a harmful pest by coffee farmers in Chiapas (Barrera *et al.* 2003, Segura *et al.* 2004).

Several groups of both vertebrate and invertebrate predators may contribute to relatively low pest occurrence in shaded coffee plantations. Several studies have documented significant effects of vertebrate predators (*e.g.*, birds, lizards, bats) on arthropods and pests in coffee agroecosystems (Perfecto *et al.* 2007, Williams-Guillen *et al.* 2008). Bird predation on insects, in particular, may be greater in plantations with diverse shade compared with monospecific shade likely due to increased abundance of an important insectivorous bird species (Perfecto *et al.* 2004). Furthermore, predatory effects of birds on arthropod populations in agroforests increase where bird diversity is greater (Van Bael *et al.* 2008).

Abundance and diversity of predatory arthropods, such as ants, may also be important in controlling populations of coffee pests. Ants are extremely important biological control agents in a number of different agricultural systems including in coffee agroforests (Philpott & Armbrrecht 2006). Among invertebrate predators, increases in diversity are often correlated with increased predation (*e.g.*, Cardinale *et al.* 2003), but conclusive evidence for effects of multiple ant species is lacking. Several recent studies have demonstrated the importance of ants in reducing the occurrence of infestations of

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the coffee berry borer (*Hypothenemus hampei* Ferrari [Coleoptera: Curculionidae]), especially in vegetatively complex agroforests (Armbrecht & Gallego 2007, Perfecto *et al.* 2007). Arboreally foraging ants, including those that inhabit coffee plants, are likely to be those with the greatest impact on potential coffee pests. For example, canopy dominant species are important pest control agents in coffee agroecosystems, with a recent emphasis placed on the role of *Azteca instabilis* Fr. Smith (Hymenoptera: Formicidae) as a keystone predator (Vandermeer & Perfecto 2006). This ant can remove introduced larvae from coffee plants faster than other canopy dominants can (Philpott *et al.* 2008), and is associated with lower incidence of the coffee berry borer (Perfecto & Vandermeer 2006). Furthermore, twig-nesting ants (Hymenoptera: Formicidae) including *Pseudomyrmex* spp., *Nesomyrmex* spp., *Crematogaster* spp., *Procryptocerus* spp., etc., live in dry, hollow twigs on coffee within plantations. Several species of these and other ant genera have been documented as important natural enemies of the coffee leaf miner, preying on eggs, larvae, and pupae of the pest in Chiapas (Lomeli Flores 2007). That study also documented that those species observed preying on eggs were not observed preying on leaf miner larvae or pupae and vice versa, and that species differed in terms of diurnal versus nocturnal predatory activities (Lomeli Flores 2007). Thus the potential exists that complementarity in diet or foraging behaviors among ant species may lead to increased effects on leaf miners where more ant species are present. Because the leaf miner is essentially sessile during its egg, larval, and pupal stages, studies involving this pest species may provide a window into the capacity of twig-nesting ants to impact both pest and nonpest insects. Unlike mobile herbivores (*e.g.*, beetles) where interpatch dispersal can mask any effects of the ants, leaf miner populations and impacts of ants on those populations can be inferred by damage to the plant on which eggs are laid and hatch.

Based on this background, we examined the relationships between predatory ants, including both *A. instabilis* and twig-nesting ant species, and damage caused by the coffee leaf miner in coffee agroecosystems in Chiapas, Mexico. We conducted surveys in areas differing in shade management to assess leaf miner damage as a function of vegetation characteristics, twig-nesting ant abundance and diversity, and presence of the canopy dominant *A. instabilis*. Specifically, we examined whether incidence and degree of leaf miner damage in coffee leaves is affected by canopy cover, tree diversity, tree density, presence of *A. instabilis*, and abundance and/or diversity of twig-nesting ants.

METHODS

Our research was conducted at Finca Irlanda (15° 11' N, 92° 20' W; 900 m asl; 4500 mm rain/yr), an organic, shaded coffee farm in the Soconusco region of SW Chiapas, Mexico. This organic farm covers 300 ha and maintains about 1200–2500 coffee plants/ha. The shade canopy at Finca Irlanda is diverse (> 60 species), but is dominated by *Inga micheliana* Harms (Fabaceae: Mimosoideae) and *Alchornea latifolia* Swartz (Euphorbiaceae).

We established 10 × 3 m transects in areas around *I. micheliana* ($N = 14$) and *A. latifolia* ($N = 15$) shade trees during June and July 2007. Transects (one per focal shade tree) extended away from the tree trunk, and the direction of each transect was selected randomly among the eight cardinal and intercardinal directions. We selected trees such that *A. instabilis* was present in half of the transects around *I. micheliana* trees ($N = 7$) and in just over half of the transects with *A. latifolia* ($N = 8$). We chose transect locations randomly from a list of tagged trees occurring in a 45-ha plot on the farm, but required that all *A. instabilis* nests had been active for at least 2 yr, and that trees were separated by a minimum of 30 m. The minimum distance between transects was 32.4 m and maximum distance between transects was 870 m. All but four transects were separated by at least 50 m. The mean distance between study transects was 356 m (± 8.33 SE). In each transect, we surveyed for presence of *A. instabilis*, presence, abundance, and identity of twig-nesting ant species, and leaf miner damage to coffee plants. Establishing transects in areas with *A. instabilis* was important because previous research has shown this species to have major impacts on species composition and overall abundance of the twig-nesting ant community (G. Livingston, S. M. Philpott, unpubl. data). To ensure that *A. instabilis* was still active on selected trees, we used visual surveys, because the ant is easy to detect after minimal disturbance to coffee plants or by lightly tapping shade tree trunks with a log.

We collected data on several vegetation characteristics in 25 × 25 m plots surrounding around each focal shade tree as potential correlates of leaf miner damage. First, we measured the percent canopy cover using a GRS vertical tube densiometer (Forestry Suppliers, Inc. Jackson, Mississippi). We measured canopy cover at four points located 5 m from each focal shade tree in the four cardinal directions. For each observation point, we estimated the total area covered with tree foliage viewed through the densiometer (held at 1.37 m aboveground) and calculated average percent canopy cover across the four points surrounding each focal shade tree. Within the 25 × 25 m plots surrounding each focal shade tree, we examined the total number of surrounding trees (> 10 cm dbh), the species richness of surrounding trees, and the percent of trees belonging to the genus *Inga*. We then examined whether these vegetation characteristics (canopy cover, tree density, tree diversity, and composition of *Inga*) were correlated with leaf miner damage to examine for relationships between shade management and occurrence of this pest.

We sampled all coffee plants within the transects for twig-nesting ants. For each coffee plant, we removed every dry twig, snapped it open, and examined it for ants. We defined occupied nests as twigs in which we found any workers, pupae, larvae, or reproductive individuals. For each occupied twig we recorded ant species identity and calculated the total number of occupied twigs and species richness in each transect (G. Livingston, unpubl. data). We identified ant species using a photographic guide for the study sites (S. M. Philpott, unpubl. data) and other published field guides for Neotropical ants (Fernández 2003, Longino 2007).

On the same plants surveyed for ants, we also sampled for leaf miner damage during July–August 2007. These dates correspond to the time of year during which the proportion of mined leaves in the region is highest (Lomeli Flores 2007). On every coffee plant, we selected three branches with stratified random selection; one on the top, one in the middle, and one at the bottom each facing in the same direction as the transect. On every branch we counted the total number of leaves, the number of mined leaves, and the percentage of damage to every mined leaf on a scale from 0 to 5. The degree of damage was characterized as follows: (0) no damage by leaf miner; (1) 0–5 percent leaf mined; (2) 5–10 percent leaf mined; (3) 10–20 percent leaf mined; (4) 20–30 percent leaf mined; and (5) 30–40 percent leaf mined. No leaves had > 40 percent mine damage.

DATA ANALYSIS.—To examine the relationships between miner damage and vegetation characteristics, *A. instabilis* presence, and abundance and diversity of twig-nesting ants, we examined both incidence of leaf miner damage (proportion of leaves with damage) and the severity of leaf miner damage (based on the damage scale). For miner incidence, we calculated proportion of surveyed leaves damaged on each branch, and took the mean proportion of damaged leaves on each coffee plant, then the mean for each transect. For severity of miner damage, we calculated mean damage level for each branch using raw values for leaf damage (0–5), and took the mean for each coffee plant, then the mean for each transect. We transformed data for proportion of leaves damaged by taking first the square root then arcsine.

To examine whether differences in vegetation characteristics related to leaf miner damage, we used multiple linear regressions with canopy cover, tree density per plot, tree species richness, and proportion of trees in the genus *Inga* as independent variables and with proportion of leaves with miner damage and mean damage level as dependent variables. Values for the proportion of *Inga* in each plot were transformed by taking first the square root then arcsine. All other untransformed variables met conditions of normality. We examined the *post-hoc* statistical power of the regressions with Statistics Calculators version 2 (Soper 2008).

We examined whether presence of *A. instabilis* influenced leaf miner damage by comparing incidence and severity of damage on plants around shade trees by using simple *t*-tests to compare plants with and without *A. instabilis*.

We used simple linear regressions to examine relationships between incidence and severity of miner damage and number of twig-nesting ant nests and twig-nesting ant species that were found around that same shade tree. Because the number of ant colonies differed in each transect, we also examined relationships between rarefied richness and miner damage. We used EstimateS 8.0 (Colwell 2005) software to rarefy our species richness data. The sampled tree with the lowest number of ant colonies (one) was used as a benchmark to compare across sites with variable abundances of ant colonies. Using output from EstimateS, we used the observed species richness (SOBS) to compare richness across different transects. We set EstimateS to 50 randomizations per calculation without replacement.

RESULTS

The vegetation differed across sampled areas of the farm, but no vegetation characteristics correlated with leaf miner damage. Canopy cover surrounding focal trees varied from 2.5 to 93.5 percent. The number of trees per plot ranged from six to 29, and tree species richness from three to 11. The percent of trees belonging to the genus *Inga* ranged from 18 to 87 percent. We found no significant relationships between the proportion of leaves with miner damage and vegetation characteristics overall ($N = 29$, $R^2 = 0.095$, $P = 0.65$) or for canopy cover ($P = 0.60$), tree density ($P = 0.76$), tree richness ($P = 0.71$), or with percent of trees in the genus *Inga* ($P = 0.51$). Mean levels of miner damage on leaves did not correlate with any vegetation characteristics ($N = 29$, $R^2 = 0.085$, $P = 0.70$) or for canopy cover ($P = 0.56$), tree density ($P = 0.77$), tree richness ($P = 0.58$), or with percent of trees in the genus *Inga* ($P = 0.52$). The observed statistical power of regressions was 0.859 for miner incidence and 0.870 for miner damage severity, thus the probability of a Type II error is above the recommended 0.80 cutoff (Cohen 1988).

The presence of *A. instabilis* did not affect presence of leaf miner attack or the extent of damage, but twig-nesting ants were associated with lower leaf miner damage. The percent of leaves with damage on plants with *A. instabilis* (5.00 ± 1.26 SE) and on plants without *A. instabilis* (6.19 ± 1.00) did not significantly differ ($t = 1.12$, $df = 27$, $P = 0.27$). The mean damage level on plants with *A. instabilis* was 0.11 ± 0.07 and on plants without *A. instabilis* was 0.08 ± 0.02 , and mean damage levels did not differ depending on presence of this ant ($t = 0.838$, $df = 27$, $P = 0.42$). In contrast, the number of twig-nesting ant nests was negatively correlated with leaf miner presence damage level (Fig. 1). The relationship between number of ant nests and percent of damage was still significant with the outlier (nest number = 52) removed ($R^2 = 0.201$, $P = 0.017$), but damage level was not ($R^2 = 0.088$, $P = 0.125$). There was no significant relationship between twig-nesting ant species richness ($N = 29$, $R^2 = 0.1245$, $P = 0.06$) or rarefied richness ($N = 29$, $R^2 = 0.1207$, $P = 0.06$) and incidence of leaf miner damage. Nor was there a significant relationship between twig-nesting ant richness ($N = 29$, $R^2 = 0.038$, $P = 0.31$) or rarefied ant richness ($N = 29$, $R^2 = 0.029$, $P = 0.38$) and severity of leaf miner damage.

DISCUSSION

Although *A. instabilis* is thought to be a keystone species in many interactions involving arthropods in coffee agroecosystem, we did not find any relationships between presence of the coffee leaf miner and *A. instabilis* presence. Both *A. instabilis* and twig-nesting ant species observed are predacious ants, but there may be strong effects of *A. instabilis* presence on diversity and abundance of twig-nesting ants (G. Livingston & S. M. Philpott unpubl. data, S. M. Philpott unpubl. data). Thus, presence of *A. instabilis* may be important, but changes in the abundance or diversity of

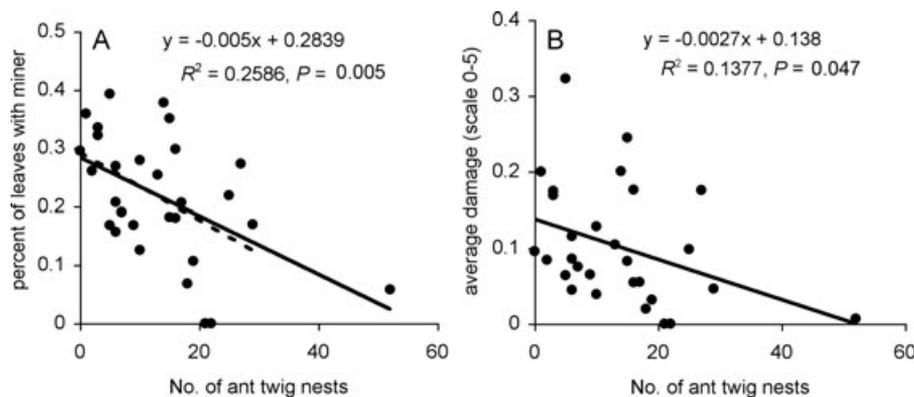


FIGURE 1. Relationships between number of twig-nesting ant nests and incidence (A) and severity (B) of leaf miner damage on coffee leaves. Percent of damaged leaves is displayed as arcsin transformed values. Severity of leaf miner damage was measured on a scale of 0–5 where 0 = no damage, 1 = 0–5 percent, 2 = 5–10 percent, 3 = 11–20 percent, 4 = 21–30 percent, and 5 = 30–40 percent damage. Each point in each panel represents a transect sampled for both miner damage and twig-nesting ants. Statistical results show simple linear regressions for each pair of variables. The dotted line shows the trend line for the regression without the outlier.

twig-nesting ants on plants where *A. instabilis* is absent could possibly mask the effects of *A. instabilis* at the local scale. The lack of effects of *A. instabilis* on leaves damaged by the leaf miner may also reflect that *A. instabilis* primarily relies on sugar resources. As such, reductions in berry borers and other pest populations by *A. instabilis* in coffee plantations may be mainly due to indirect effects on herbivorous insects (e.g., knocking herbivores off plants, changing herbivore foraging behavior) rather than direct predation. For example, Perfecto and Vandermeer (2006) found that density of scale insects (actively tended by *A. instabilis*) negatively correlated with proportion of fruits attacked by the coffee berry borer.

We did not observe significant relationships between leaf miner damage levels and vegetation characteristics. The impact of shade cover or other vegetation variables such as tree density and tree richness might also only be detectable at larger spatial scales. Because this is an organic plantation, this result may also indicate that the increases in leaf miner populations in some intensive farms is more strongly linked to secondary outbreaks following pesticide application rather than to changes in microclimate conditions. Such a prediction could be examined by comparing leaf miner outbreaks in organic and pesticide-using conventional farms managed similarly in terms of canopy cover and other shade characteristics. However, given that several previous studies have found influences of microclimate and other site characteristics on leaf miner outbreaks (e.g., Lomeli Flores 2007, Pereira *et al.* 2007), our results should be treated with caution.

The observed relationship between the abundance of twig-nesting ant nests and leaf miner damage suggests that twig-nesting ants may play an important role in the control of this pest in shaded coffee agroecosystems. Ants may affect the leaf miner in one of several ways. First, ants are aggressive toward herbivores and parasitoids, and this aggression or even simply presence of ants on coffee leaves may affect the oviposition behavior of the leaf miner adults as has been seen for other nonmyrmecophilous butterflies (Freitas & Oliveira 1996). Second, ants may prey on eggs, larvae, or pupae of the leaf miners (Lomeli Flores 2007). Such a mode of control

is consistent with the apparent absence of chitin in the nests of all twig-nesting species suggesting that the ants only feed on soft-bodied prey (G. Livingston, pers. obs.). Thirteen species of several ant genera (*Pseudomyrmex*, *Nesomyrmex*, *Brachymyrmex*, *Camponotus*, and *Cephalotes*) feed on various leaf miner life stages (Lomeli Flores 2007). In this work, Lomeli Flores (2007) documented only a few ant species that fed on multiple life stages (e.g., eggs plus larvae) and that some species preyed on leaf miners nocturnally whereas other predatory activities took place during the day. Such species differences in foraging behaviors and prey items may indicate that there is niche differentiation or complementarity among predators in this assemblage, ultimately leading to enhanced predatory effects where more twig-nesting ant species are present (e.g., Hooper *et al.* 2005). In this study, we did not find significant relationships between twig-nesting ant diversity and leaf miner damage. Nevertheless, future controlled studies will be able to elucidate the ways in which different genera or species of ants affect the miner, and whether the effects of different ants complement one another or are redundant in their effects on pests. However, the R^2 values for both regressions examining the relationship between leaf miner damage and ant abundance were rather low (0.26, 0.14) indicating that there is substantial variation in the relationship. We feel that this is to be expected in highly complex communities such as this coffee farm. Ants are certainly not the only predator of leaf miners, and ants may indeed have negative effects on leaf miner parasitoids or on other predators such as spiders. The degree to which different ant species prey on leaf miners, and display aggressive behaviors against other predators and parasites may contribute to this variation in the relationship.

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