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Wood-Nesting Ants and Their Parasites in Forests and Coffee Agroecosystems

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ABSTRACT Agricultural intensification is linked to reduced species richness and may limit the effectiveness of predators in agricultural systems. We studied the abundance, diversity, and species composition of wood-nesting ants and frequency of parasitism of poneromorph ants in coffee agroecosystems and a forest fragment in Chiapas, Mexico. In three farms differing in shade management and in a nearby forest fragment, we surveyed ants nesting in rotten wood. We collected pupae of all poneromorph ants encountered, and incubated pupae for 15 d to recover emerging ant parasites. If no parasites emerged, we dissected pupae to examine for parasitism. Overall, we found 63 ant morphospecies, 29 genera, and 7 subfamilies from 520 colonies. There were no significant differences in ant richness or abundance between the different sites. However, there were significant differences in the species composition of ants sampled in the four different sites. The parasitism rates of ants differed according to site; in the forest 77.7% of species were parasitized, and this number declined with increasing intensification in traditional polyculture (40%), commercial polyculture (25%), and shade monoculture (16.6%). For three of four poneromorph species found in >1 habitat, parasitism rates were higher in the more vegetatively complex sites. The result that both ant species composition and ant parasitism differed among by site indicates that coffee management intensification affects wood-nesting ant communities. Further, coffee intensification may significantly alter interactions between ants and their parasites, with possible implications for biological control in coffee agroecosystems.

KEY WORDS agroforest, biodiversity, Eucharitidae, poneromorph, trophic interaction

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Loss of habitat contributes to species extinction, especially in tropical regions. One of the principal reasons for the deterioration of natural habitats is expansion and intensification of agriculture (Vandermeer and Perfecto 2005). However, some agricultural habitats, such as shaded coffee agroforests, maintain high levels of biodiversity of mammals, birds, reptiles, and arthropods (e.g., Perfecto et al. 1996, Moguel and Toledo 1999, Perfecto et al. 2003, Philpott et al. 2008). For example, traditional shaded coffee farms contain a high diversity of ants, spiders, and hymenopteran parasitoids (Perfecto and Snelling 1995, Perfecto and Vandermeer 1996, Ibarra-Núñez et al. 2001, Armbrecht et al. 2005). However, in recent years, these diverse agroecosystems have been transformed into homogeneous monocultures for the purpose of increasing yields (Perfecto et al. 1996, Soto-Pinto et al. 2000). Studies comparing sun coffee with shaded coffee agroecosystems varying in vegetation complexity generally show that technification (elimination and simplification of shade and increases in agrochemical use) results in a loss of biodiversity for the many taxa evaluated (Perfecto et al. 1996, Brown et al. 2001, Armbrecht and Perfecto 2003, Perfecto et al. 2007, Philpott et al. 2008).

Ants have frequently been used as indicator species to examine the effects of coffee management intensification on biodiversity in disturbed landscapes (Majer 1986), but few studies have examined ants that live in rotting wood, an abundant habitat in tropical forests. In tropical regions, ants are diverse, abundant, and inhabit a variety of ecological niches (Hölldobler and Wilson 1990, Rojas-Fernández 2001, Brown et al. 2001). In coffee agroecosystems, the loss of shade trees may produce a shortage of nesting sites such as twigs, seeds, leaf-litter, and bark, leading to reduced ant diversity or abundance of arboreal ants, and of ants that live in the twigs or spaces in leaf litter (Armbrecht et al. 2004, Philpott and Foster 2005). Less well-studied are the numerous ant species that live in small colonies occupying fragile, short-lived nest sites like rotten wood (Morón et al. 1988, Byrne 1994). The removal or cutting of shade trees, and harvesting of fire wood by coffee workers may affect the availability of rotting wood, and the different temperature and moisture conditions in coffee agroecosystems varying in management intensity may affect decomposition rates of fallen logs that remain in the agroecosystem.

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Rotting wood provides an important nesting site and resource to several tropical genera of ants including *Solenopsis* (Wagneri), *Pseudomyrmex* (Lund), *Camponotus* (Mayr), *Pachycondyla* (Smith), and *Odontomachus* (Latreille) (Morón et al. 1988, Lachaud and García-Ballinas 2001). In cacao and coffee agroforests in Mexico, Lachaud and García-Ballinas (2001), found 28 ant species distributed in 12 genera in the poneromorph and Cerapachyinae subfamilies nesting in rotten logs, but there are no studies that have examined how diversity or species composition of wood-nesting ants compares in forests and agroforests varying in management intensity.

In addition to the impacts on ant diversity, tropical agriculture practices can also affect the interactions between ants and ant parasites, and ant prey. Ants play important roles in trophic interactions in agroecosystems (Perfecto et al. 2003). First, ants are important predators in several agroecosystems (Way and Khoo 1992, Philpott and Armbrecht 2006). Specifically in coffee plantations, ants prey on two important coffee pests, the coffee berry borer (*Hypothenemus hampei* Ferrari) and the coffee leaf miner (*Leucoptera coffeella* Guerin-Meneville) (Armbrecht and Gallego 2007, De la Mora et al. 2008), and have important impacts on other herbivores (Varón et al. 2004, Perfecto and Vandermeer 2006, Philpott and Armbrecht 2006, Armbrecht and Gallego 2007, De la Mora et al. 2008). Thus, ants may provide a variety of pest control services within coffee agroecosystems (Delabie et al. 2003), but their function may depend on overall ant abundance or diversity (Philpott and Armbrecht 2006, De la Mora et al. 2008). Second, agricultural intensification may affect the relationship of ants with their predators and parasites, but few have studied the importance of the interactions between ants and ant parasites in agroecosystems. Coffee intensification can reduce the abundance and diversity of parasitoid wasps (Tylianakis et al. 2005, 2007, S. Uno, unpublished data). However, few studies have examined specifically the diversity of ant parasites and their abundance in natural or in agricultural systems (Johnson et al. 1986, Pérez-Lachaud et al. 2006b, Lachaud and Pérez-Lachaud 2009).

Ants have several natural enemies including both dipteran and hymenopteran parasitoids (Heraty 1994, Feener 2000). Eucharitidae are specialized parasitoids of ants (Heraty and Darling 1984, Johnson 1988, Heraty 1994, Heraty et al. 2004). Females deposit between 10,000–15,000 eggs during their lifetime (Johnson 1988), with different species using different plant tissues like flower buds and leaves (Clausen 1940) where the ant host is likely to forage (Howard et al. 2001, Pérez-Lachaud et al. 2006a). The first larval instars, the planidia, attach to foraging ant adults for phoretic transport to the ant nest (Clausen 1940, Heraty 2000) where they then parasitize ant brood (Clausen 1941, Johnson et al. 1986). Several genera of eucharitid wasps are reported to attack poneromorph ants in Chiapas including *Dilocantha* (Shipp), *Kapala* (Cameron), and *Isomerala* (Cameron) (Lachaud et al. 1998, Pérez-Lachaud et al. 2006a, b, Lachaud and Pérez-Lachaud 2009). *Kapala* and *Isomerala* are specifically known to attack *Ectatomma tuberculatum* (Olivier) (Lachaud et al. 1998, Pérez-Lachaud et al. 2006b). Based on the limited observations available of *Kapala* oviposition behavior, specifically, different species tend to use different plant parts, and the 4 species observed used host plants from 7 different families (Pérez-Lachaud et al. 2006a). Thus complex habitats, such as diverse traditional polyculture coffee farms, may provide resources necessary for maintaining populations of a diverse assemblage of eucharitid ant parasitoids.

We examined how differences in coffee management intensity, namely changes in the shade canopy above the coffee plants, affect ants that nest in rotting wood and further examined parasitism of one subset of wood-nesting ants by eucharitid wasps. Specifically, we investigated differences in the diversity, species composition, and relative abundance of wood-nesting ants in three coffee management systems and nearby forest fragments. Then, for group of these ants, the poneromorph subfamilies (Ponerinae and Ectatomminae), we examined pupal parasitism rates and diversity of parasites collected from these host ants.

Materials and Methods

Field Site. We conducted our study between August 2007 and July 2008 in 2 coffee farms and one forest fragment in the Soconusco region of Chiapas, Mexico. The 2 farms were: (1) Finca Irlanda (15° 11′N, 92° 20′W; 900 masl) and (2) Finca Hamburgo (15° 10′N, 92° 19′W). Both farms receive ≈4,500 mm rain/yr. Finca Irlanda is an organic farm and contains two distinct management areas: a traditional polyculture (TP) area that covers ≈20 ha and a commercial polyculture (CP) that covers ≈250 ha. The entire farm is 300 ha and maintains ≈1,200–2,500 coffee plants/ha. Finca Hamburgo is a conventional shade monoculture (SM) farm with ≈280 ha in coffee production. These three sites represent a gradient of management intensity from the TP site with the highest diversity and density of shade trees and canopy cover to the SM site, with the fewest trees and the lowest canopy cover levels. The description of the sites follows Philpott et al. 2008 where TP has between 10–20 tree species and 60–90% canopy cover, CP has 5–10 tree species and 30–60% canopy cover, and SM has 1–5 tree species and <30% canopy cover and together encompass the full range of coffee management types in the immediate region. Each of the habitat areas is quite large with TP covering 7 ha, CP covering 200 ha, SM covering 1,000 ha. Additionally, located between the 2 farms is a small biological reserve, "La Montañita," a typical montane forest (F), with large trees and patches of second growth, that was included as a natural forest site covering 15 ha. In every site where ants were collected, we measured the percent canopy cover using a GRS 129 vertical tube densiometer (Forestry Suppliers, Inc., Jackson, MS).

Ant Survey and Analysis. We sampled ants nesting in rotten wood using a series of transects. To standardize the effort in each habitat type, we walked 4-h transects each month for 12 mo searching for rotten logs. Each month, a new haphazardly selected area of the habitat type was sampled. In SM and CP each transect was separated by a minimum of 200 m, whereas in TP and F, because of the smaller sizes of the overall habitat, transects were separated by only 100 m. Upon encountering a rotten log, we used machetes and axes to first pry off the bark, and then to fragment the trunk while searching for ants. We collected specimens of all ant species encountered, and placed them into vials filled with 70% ethanol, where they were stored for later identification. We identified ant species using field guides for the study sites (Philpott 2008), expert's lists of ants that are known to occur in Chiapas (Longino 2009) and other published guides for neotropical ants (Fernández 2003, Longino 2007).

To examine the abundance of wood nesting ants in the different sites, we compared the number of occurrences per 4-hr transect with univariate analysis of variance (ANOVA). For the ANOVA, we used the number of occurrences during each monthly survey as the dependent variable, different survey months (and hence locations) as the replicate, and site type (forest, TP, CP, or SM coffee) as the independent variable and compared pair-wise differences using Tukey's tests. Because habitat types were not replicated, significant differences in the ANOVA can only be interpreted as differences between sites, not necessarily differences between habitat types. We compared the species richness of ants in the different habitat types with EstimateS 7.5 (Colwell 2005). We created species accumulation curves for observed richness (MaoTao) and for estimated species richness with Chao2 and ICE. For creating accumulation curves, we used presence/absence data for each sample rather than abundance data because ants are colonial (Longino et al. 2002).

To examine whether the species composition of wood nesting ants differed in the 4 different sites we used 3 methods. First, we calculated similarity in the species composition of ants among different sites using the Bray-Curtis similarity index (see Krebs 1989). Second, we conducted a nonmetric multi-dimensional scaling (NMDS). For the NMDS, we created a matrix of abundance of each species in each microhabitat per site, and then used the Bray-Curtis similarity index as the similarity measure to graphically compare the similarity of each transect within habitat. Each run was conducted with 10,000 permutations. Third, we used the Analysis of Similarities (ANOSIM) with PAST (Hämmer et al. 2001) to statistically compare the similarity of the species found in each site. ANOSIM produces a global *P* value to determine whether any species compositions differ, and also conducts pair wise comparisons between particular sites. For NMDS and ANOSIM, we examined each 4-hr transect as a replicate within site, and examined species composition based on ant occurrences.

Parasitoid Sampling and Analysis. We sampled ant parasitoids by collecting pupae in the field and rearing parasitoids in the lab. Each time that we encountered a colony of poneromorph ants (Ectatomminae and Ponerinae) during the ant surveys, we collected ≈10% of the total pupae visible in the colony and took these pupae to the lab to rear parasitoids. We placed all pupae from the same colony into a plastic cup covered with mesh to allow air into the cup, but to prevent the escape of emerged parasitoids. Because the pupal stage of some Eucharitidae is 13 d for females and 7 d for males under laboratory conditions (Pérez-Lachaud et al. 2006a), we kept cups from each colony for a total of 15 d, and checked every day for the presence of parasitoid adults inside the cups. After 15 d the puparia were dissected to examine for parasitoid larvae or pupae.

We examined patterns of ant parasitism in 2 ways. First, we recorded which ant species were parasitized in each habitat type, and the fraction of species that were parasitized to document basic natural history of ant-parasite interactions in coffee agroecosystems. Second, to look at changes in parasitism rate as a result of agricultural intensification, we compared the fraction of colonies of the same species that were parasitized in the different sites. The latter necessitated only examining those ant species that were found in 2 or more sites.

Results

Ant Abundance, Richness, and Composition. We collected a total of 63 ant morphospecies from a total of 520 colonies in the four habitats. We found 37 species and 124 colonies (from 89 logs) in the forest, 33 species and 134 colonies (from 136 logs) in TP coffee, 33 species and 118 colonies (from 99 logs) in CP coffee, and 36 species and 144 colonies (from 104 logs) in SM coffee (Fig. 1; Table 1). The species of *Cerapachys* (Smith) encountered and at least 4 species of *Pheidole* encountered are undescribed (J. Lattke and J. T. Longino, personal communication). There were 10.33 ± 1.02 (SE) colonies per 4-hr transect in the forest, 11.17 ± 1.01 in TP, 9.83 ± 0.64 in CP, and 12.0 ± 0.59 in SM. There were no significant differences in the abundance of colonies found during 4-hr searches in different sites (F (3, 44) = 1.235, P = 0.308). There were no significant differences between observed or estimated richness for any pairs of forest or coffee sites as indicated by examining overlapping 95% confidence intervals (CI) between all pairs of sites (CIs are not plotted here for clarity) (Fig. 1).

In the different sites, the most abundant species, in terms of percent of total occurrences was *Pachycondyla stigma* (F.) that accounted for 13.1% of occurrences overall and 14.5% of occurrences in the forest, 7.5% in TP, 21.2% in CP, and 10.4% in SM. The second most common species overall was *Gnamptogenys striatula* (Mayr) with 10.2% of total occurrences and 10.5% of occurrences in the forest, 10.2% in CP, and 12.5% in SM. One species of *Pheidole* (sp. 9) accounted for 8.1% of overall occurrences and for 14.5% in the forest, 9.0% in TP, and 6.9% in SM. Other species that were common in only one site included *G. sulcata* (Smith) (13.4% of colonies in TP), *Strumigenys biolleyi* (Forel)

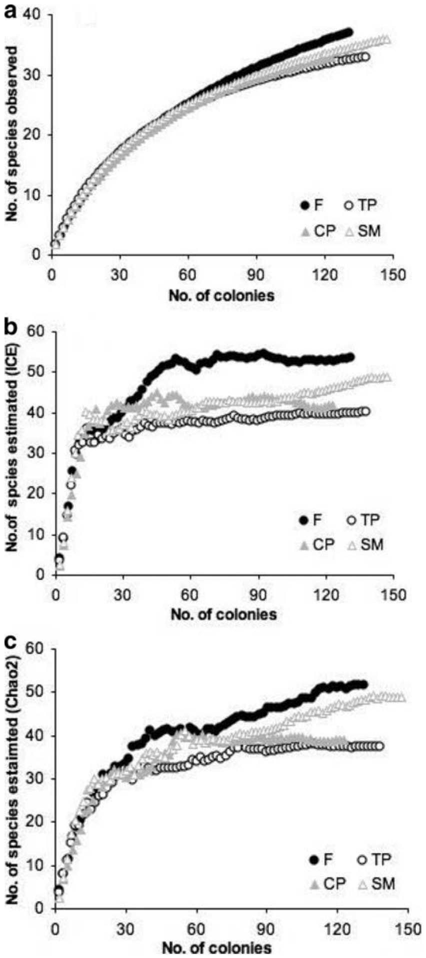

Fig. 1. Species accumulation curves showing richness of ants nesting in rotten logs in a forest fragment (F) and in three coffee management systems varying in canopy complexity (TP = traditional polyculture coffee, CP = commercial polyculture coffee, SM = shade monoculture coffee). Graphs show observed species richness (a), and estimated species richness calculated with the ICE (b) and Chao2 (c) estimators in EstimateS.

(6.8% of colonies in CP), *Crematogaster* sp. 1 (6.9% of colonies in SM), and *Typhlomyrmex rogenhoferi* (Mayr) (5.9% of colonies in CP).

In general, only about half of the species found in the forest were also found in the coffee sites and there were significant differences in the species composition of ants encountered in the four different sites. According to the Bray-Curtis Similarity Index, the forest was most similar to CP and most different from TP (Table 2). There was generally higher overlap among coffee sites with CP and SM and most similar to each other and CP and TP least similar (Table 2). The graphical view of species composition from the NMDS shows distinct groups of species in each site (Fig. 2). Finally, the ANOSIM showed highly significant differences overall (Global $R = 0.1757$; $P < 0.0001$) and between pairs of sites. The forest community was distinct from TP ($P < 0.001$), from CP ($P = 0.009$), and from SM ($P < 0.001$). The TP coffee ant community was significantly different than CP ($P = 0.014$) and SM ($P = 0.035$) and CP and SM had distinct ant communities ($P = 0.004$).

Ant Parasitism. We encountered a total of 240 poneromorph (97 Ectatomminae and 143 Ponerinae) colonies in the 4 habitat types, but only 64 of them had pupae. From these 64 colonies, we collected and incubated a total of 1791 poneromorph pupae from which a total of 34 adult eucharitid parasitoids emerged. Additionally, in the dissections of the rest of the total puparia incubated, 40 eucharitid pupae and nine immature adults were found. A total of 23 colonies of the 64 from which pupae were recovered were parasitized. All of the eucharitids encountered belonged to the genus *Kapala*, but no species-level identifications were made. We collected 13 species of poneromorph ants, 8 from which we collected parasitoids (Table 3). For 5 of those species, more than half of colonies encountered were parasitized. All colonies of *Odontomachus laticeps* (Roger), *P. apicalis*, and *T. rogenhoferi* were parasitized; 53.85% of *Odontomachus meinerti* (Forel) colonies were parasitized, and 50.0% of *G. sulcata* colonies were parasitized. In the forest, we found eucharitid parasites from at least one colony of seven of the nine species collected (77.7%). The fraction of parasitized ant species declined with management intensification with 2 of 5 (40%) species parasitized at least once in TP, 1 of 4 species parasitized in CP (25%), and only 1 of 6 (16.6%) species parasitized in SM.

From all surveys, there were only 4 species of poneromorph ants that were found in more than one habitat type (*G. sulcata, O. meinerti, P. stigma* F., and *P. harpax* F.), and the number of colonies collected was small. Thus, our ability to compare parasitism rates in different sites was somewhat limited. As preliminary patterns, for all of the 4 species that were found in more than one site, with the exception of *G. sulcata*, a higher fraction of their colonies were parasitized in the forest or more vegetatively complex coffee site (TP) than in the more intensive coffee sites (CP and SM) (Table 3).

Discussion

We found relatively high richness of ants nesting in rotten logs in both forests and coffee agroecosystems and there were no significant differences in abundance and richness of these ants depending on the site. Nonetheless, we found >60 ant species overall, many of which have not yet been documented from the study region, and some that may be new species. Generally, ant species from rotting wood have been less studied in agroforests, and even after several years of ant research at the study sites, we collected many new species. Furthermore, there were several species (e.g., *Cerapachys* sp. 1, *P. impressa* (Roger), *Pheidole* sp. 2) and one genus, *Leptogenys* (Roger), that were only encountered in the forest and could be used in

Table 1. Ant colonies encountered nesting in rotten logs on the ground in a forest fragment (F) and in three coffee management systems varying in canopy complexity

Subfamily	Species	F	TP	CP	SM
Cerapachyinae	*Cerapachys* sp. 1	2	0	0	0
Ecitoninae	*Labidus* cf. *coecus*	0	0	3	1
Ectatomminae	*Gnamptogenys striatula*	13	10	12	18
Ectatomminae	*Gnamptogenys sulcata*	0	18	4	1
Ectatomminae	*Typhlomyrmex rogenhoferi*	2	5	7	7
Formicinae	*Brachymyrmex* sp. 1	1	7	5	6
Formicinae	*Brachymyrmex* sp. 2	0	0	1	3
Formicinae	*Camponotus* sp. 1	0	0	0	1
Formicinae	*Camponotus* sp. 2	1	0	0	0
Formicinae	*Camponotus* sp. 3	0	2	2	2
Formicinae	*Camponotus* sp. 4	0	0	0	1
Formicinae	*Camponotus* sp. 5	0	0	0	1
Formicinae	*Camponotus* sp. 7	0	0	0	1
Formicinae	*Camponotus* sp. 8	0	0	0	1
Formicinae	*Myrmelachista* sp. 1	0	3	2	7
Formicinae	*Paratrechina* sp. 1	2	1	0	4
Myrmicinae	*Acromyrmex* sp. 1	1	0	1	0
Myrmicinae	*Cardiocondyla* sp. 1	1	3	1	2
Myrmicinae	*Carebara* sp. 1	1	0	1	0
Myrmicinae	*Crematogaster* sp. 1	1	5	1	10
Myrmicinae	*Cyphomyrmex opaca*	4	4	1	4
Myrmicinae	*Monomorium floricola*	0	1	0	0
Myrmicinae	*Nesomyrmex echinatinodis*	0	3	0	0
Myrmicinae	*Pheidole* sp. 1	0	0	0	1
Myrmicinae	*Pheidole* sp. 2	4	0	0	0
Myrmicinae	*Pheidole* sp. 3	0	0	0	1
Myrmicinae	*Pheidole* sp. 4	0	0	0	1
Myrmicinae	*Pheidole* sp. 5	0	0	3	0
Myrmicinae	*Pheidole* sp. 6	1	0	0	0
Myrmicinae	*Pheidole* sp. 7	0	1	0	0
Myrmicinae	*Pheidole* sp. 8	2	0	1	0
Myrmicinae	*Pheidole* sp. 9	18	12	2	10
Myrmicinae	*Pheidole* sp. 10	0	2	5	1
Myrmicinae	*Pheidole* sp. 11	1	0	2	0
Myrmicinae	*Pheidole* sp. 12	0	2	1	3
Myrmicinae	*Procryptocerus hylaeus*	1	0	0	0
Myrmicinae	*Pyramica* sp. 1	3	5	3	7
Myrmicinae	*Rogeria* cf. *tonduzi*	5	1	3	3
Myrmicinae	*Solenopsis* sp. 1	3	2	5	5
Myrmicinae	*Solenopsis* sp. 2	1	0	0	0
Myrmicinae	*Solenopsis* sp. 3	0	0	2	1
Myrmicinae	*Solenopsis* sp. 4	1	1	1	0
Myrmicinae	*Solenopsis* sp. 5	1	3	5	8
Myrmicinae	*Strumigenys biolleyi*	8	7	8	2
Myrmicinae	*Wasmannia auropunctata*	0	2	0	0
Ponerinae	*Hypoponera* cf. *opacior*	3	2	0	0
Ponerinae	*Hypoponera nitidula*	3	0	1	0
Ponerinae	*Leptogenys* cf. *pusilla*	1	0	0	0
Ponerinae	*Leptogenys* sp. 1	1	0	0	0
Ponerinae	*Leptogenys* sp. 2	4	0	1	0
Ponerinae	*Odontomachus laticeps*	2	5	3	1
Ponerinae	*Odontomachus meinerti*	2	1	2	4
Ponerinae	*Pachycondyla apicalis*	1	2	2	2
Ponerinae	*Pachycondyla cognata*	4	0	0	1
Ponerinae	*Pachycondyla harpax*	4	0	2	4
Ponerinae	*Pachycondyla impressa*	2	0	0	0
Ponerinae	*Pachycondyla* JTL 011	1	1	0	0
Ponerinae	*Pachycondyla* sp.1	0	1	0	0
Ponerinae	*Pachycondyla* sp. 2	0	1	0	1
Ponerinae	*Pachycondyla* sp. 3	0	0	0	1
Ponerinae	*Pachycondyla stigma*	18	10	25	15
Ponerinae	*Platythyrea punctata*	0	7	0	2
Pseudomyrmecinae	*Pseudomyrmex gracilis*	0	4	0	0

Numbers represent the no. of colonies found in 48 h of surveys in each habitat. F, forest; TP, traditional polyculture coffee; CP, commercial polyculture coffee; SM, shade monoculture coffee.

the future as indicator species for biodiversity conservation and monitoring (Majer 1986).

A lack of difference in richness and abundance of ants between habitat types was a surprising result given that most studies focusing on ants in coffee agroecosystems generally encounter lower ant richness (e.g., Philpott et al. 2008) and changes in ant abundance with coffee intensification (Perfecto and

Table 2. Ant species similarity between pairs of forest and coffee sites

Sites	F	TP	CP	SM
F	na	0.496	0.579	0.522
TP	< 0.001	na	0.548	0.590
CP	0.009	0.014	na	0.603
SM	0.001	0.001	0.004	na

Numbers above the diagonal show Bray-Curtis Similarity Index values. Numbers below the diagonal show *P* values for pair-wise comparisons in ANOSIM. F, forest; TP, traditional polyculture coffee; CP, commercial polyculture coffee; SM, shade monoculture coffee.

Vandermeer 1996; Philpott et al. 2006). We expected to find a higher abundance of logs and ants in the more vegetatively complex habitats (e.g., forest and TP coffee). One potential reason why ant abundance and richness did not differ is because, in more intensively managed coffee farms like CP and SM, shade trees are heavily pruned. Although most of the branches that are cut from trees are removed as firewood, some may be left on the ground, mirroring natural felling of branches and trunks in more complex systems. Although we standardized surveys by time (4 h per month in each habitat), we did not record the total area covered during each transect or the specific log density per unit area in any habitat types, thus this is one limitation of the study that should be remedied in similar studies in the future. If there were differences in log density in the different sites, the area sampled may have varied with larger spaces between and thus larger area sampled in sites with lower log density. This increased area sampled could explain a lack of differences in richness between sites. One caveat that must be mentioned is that our study sites, despite representing a gradient of intensification, are only single replicates of each habitat type. They are large areas (7–200 ha in size), and because of the nature of the landscape are highly difficult to completely replicate. Because of this low replication, the data and interpretation reported here and elsewhere in the paper should be taken with caution.

Even though richness and abundance of ants was similar, there were very significant differences in species composition at each of the 4 sites. Species similarity among coffee sites was higher than between coffee and forest sites. Again, surprisingly, the species similarity between the forest and the more intensive coffee sites (CP and SM) was higher than for the coffee habitat most similar to the forest in terms of vegetation characteristics (TP). Other studies have found comparable differences in ant species composition in different sites (Byrne 1994, Armbrecht et al. 2004) as did we, but in contrast, most studies find higher degrees of similarity between forests and less intensive coffee management (e.g., Perfecto et al. 2003, Armbrecht and Perfecto 2003, Philpott et al. 2006). These differences could be because of differences in guilds of ants, as no other studies have examined diversity of wood-nesting ants in these coffee agroforests.

The preliminary results presented here on parasitism show differences in parasitism in different sites that can be attributable to several different factors. First, eucharitid parasitoids are generally host specific, parasitizing only one or a few related genera of ants (Pérez-Lachaud et al. 2006b). With different ant composition, the hosts of potential parasites, and thus parasitism rates could be expected to vary. Based on our somewhat limited data, parasitism was generally higher in the forest and TP than in the more intensive coffee sites. These results are consistent with studies examining the effect of habitat complexity on parasitism rates (Marino and Landis 1996, but see Menalled et al. 1999). On a side note, Marino and Landis (1999) also compared parasitism in a landscape without complete site replication. In some cases, parasi-

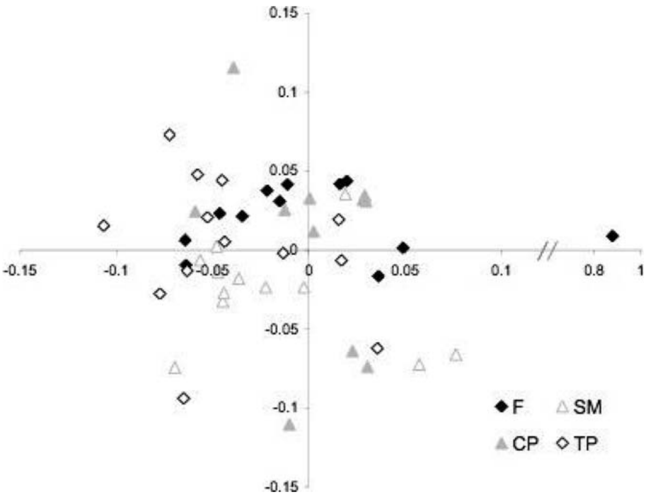

Fig. 2. Nonmetric multi-dimensional scaling analysis showing differences in species composition of wood nesting ants in a forest fragment and in three coffee management systems varying in canopy complexity (F = forest, TP = traditional polyculture coffee, CP = commercial polyculture coffee, SM = shade monoculture coffee).

Table 3. Eucharitid parasitism of poneromorph ant pupae in a forest fragment and three coffee management systems varying in canopy complexity

Species	F		TP		CP		SM	
	P	NP	P	NP	P	NP	P	NP
Gnamptogenys striatula	0	0	0	0	0	0	0	1
Gnamptogenys sulcata	0	0	5	5	0	2	2	0
Hypoponera cf. *opacior*	0	0	0	1	0	0	0	0
Hypoponera nitidula	1	3	0	0	0	0	0	0
Leptogenys sp. 1	0	1	0	0	0	0	0	0
Odontomachus laticeps	1	0	0	0	0	0	0	0
Odontomachus meinerti	3	2	3	1	1	2	0	1
Pachycondyla apicalis	1	0	0	0	0	0	0	0
Pachycondyla cf. *cognata*	0	1	0	0	0	0	0	0
Pachycondyla harpax	1	0	0	0	0	1	0	1
Pachycondyla stigma	3	4	0	1	0	10	0	1
Platythyrea punctata	0	0	0	2	0	0	0	1
Tyhplomyrmex rogenhoferi	2	0	0	0	0	0	0	0
Grand total	12	11	8	10	1	15	2	5

Numbers represent the no. of colonies from which poneromorph ant pupae were dissected and that were parasitized (P) or not parasitized (NP). F, forest; TP, traditional polyculture coffee; CP, commercial polyculture coffee; SM, shade monoculture coffee.

toids may be less effective at parasitizing ants in sites with simpler vegetation (Klein et al. 2006). Parasitoid attack rates may also be highly linked to the population size of parasitoids in each habitat type, in turn related to environmental conditions necessary for maintaining high populations. Many parasitoids require food resources other than hosts (e.g., extrafloral nectar, pollen) (Landis et al. 2000). In some cases, presence of weeds or high levels of moisture correlate with higher parasitoid populations, and such conditions relate to more efficient parasitism (Shapiro and Pickering 2000). Data from the field sites show much lower moisture levels occur in the SM and CP sites than in the forest or TP (Lin 2007). Eucharitid wasps also require specific host plants for depositing planidia. For example, *Kapala iridicolor* (Cameron), one parasitoid known from the study region, uses the aster *Melampodium divaricatum* as a preferred oviposition site, and presence of this plant is necessary for the parasitoid to complete the life cycle (Pérez-Lachaud et al. 2006a). In the study sites, understory plants (i.e., weeds) are sometimes treated with herbicides (in SM site) or are frequently cut with machetes (in CP site). In contrast, in the TP site and forest, little to no management of the weeds is conducted. Thus, the variety and abundance of potential host plants for eucharitids is likely much higher in the TP and forest than in SM or CP sites, consistent with lower parasitism rates in the latter. Finally, difference in parasitism rate could be because of physical barriers to dispersal for eucharitids. As for other ecosystem services, such as coffee pollination by bees from nearby forest fragments, parasitoid wasps may fly defined distances from the forest into coffee plantations to parasitize and it would be interesting to examine parasitism rates on ants at increasing distances from forest fragments as has been done to study ant diversity and predatory capabilities (Perfecto and Vandermeer 2002, Armbrecht and Perfecto 2003).

In contrast to previous studies of ant parasites in the Soconusco region of Chiapas, we encountered only one genus of eucharitid parasite known from the region. We encountered *Kapala* parasitoids, but not *Isomerala* and *Dilocantha* (Heraty 1998, Lachaud et al. 1998). Elsewhere in the Soconusco, at lower elevations, *E. tuberculatum* is attacked by *Isomerala coronata* (Westwood), *Dilocantha lachaudii* (Heraty), and *Kapala* spp. in coffee plantations (Lachaud et al. 1998, Pérez-Lachaud et al. 2006b), but we did not encounter any *Ectatomma* spp. pupae to examine for parasitism. Specifically in our study, we found *Kapala* parasites of *G. sulcata, G. striatula* (Mayr), and *P. stigma.* All of these species of ants are reportedly attacked by *K. iridicolor* (Pérez-Lachaud et al. 2006a). Some differences in parasitoid occurrences may be because of regional or elevational differences in ant composition.

In summary, compared with previous studies on ants in coffee agroecosystems, we did not find differences in richness or abundance of wood nesting ants, but did find strong differences in species composition. In poneromorph ants, parasitism by eucharitid parasitoids was common and somewhat stronger in the forest and TP sites, perhaps because of differences in alternative resources, host plants, or microclimatic differences. These differences in wood-nesting ants and their parasitoids may have implications for other trophic interactions involving ants in agroecosystems and for insect conservation in agricultural landscapes.

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