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Local and Landscape Drivers of Ant Parasitism in a Coffee Landscape

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ABSTRACT Parasitism of ants that nest in rotting wood by eucharitid wasps was studied in order to examine whether habitat and season influence ant parasitism, vegetation complexity and agrochemical use correlate with ant parasitism, and whether specific local and landscape features of agricultural landscapes correlate with changes in ant parasitism. In a coffee landscape, 30 coffee and 10 forest sites were selected in which local management (e.g., vegetation, agrochemical use) and landscape features (e.g., distance to forest, percent of rustic coffee nearby) were characterized. Rotten logs were sampled and ant cocoons were collected from logs and cocoons were monitored for parasitoid emergence. Sixteen ant morphospecies in three ant subfamilies (Ectatomminae, Ponerinae, and Formicinae) were found. Seven ant species parasitized by two genera of Eucharitidae parasitoids (*Kapala* and *Obeza*) were reported and some ant–eucharitid associations were new. According to evaluated metrics, parasitism did not differ with habitat (forest, high-shade coffee, low-shade coffee), but did increase in the dry season for *Gnamptogenys* ants. Parasitism increased with vegetation complexity for *Gnamptogenys* and *Pachycondyla* and was high in sites with both high and low agrochemical use. Two landscape variables and two local factors positively correlated with parasitism for some ant genera and species. Thus, differences in vegetation complexity at the local and landscape scale and agrochemical use in coffee landscapes alter ecological interactions between parasitoids and their ant hosts.

KEY WORDS coffee, eucharitidae, formicidae, vegetation complexity

Deforestation and intensification of agroecosystems contribute to global loss of diversity and to alterations in species interactions and ecosystem services provided. Ecosystem services are "the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life" (Daily 1997). In agroecosystems, richness and abundance of some organisms decrease due to habitat simplification and landscape modification (Dauber et al. 2005, García Estrada et al. 2006). Some implications of biodiversity loss are the disruption of ecological processes and alteration of interaction networks that support mutualisms and ecosystem services (Naeem 2002, Fischer et al. 2006). Species interactions are modified by landscape changes including fragmentation (Tscharntke et al. 2002), changes to matrix quality (Vandermeer and Carvajal 2001, Steffan-Dewenter et al. 2002), modifications to forest shape, edge, or area (Tscharntke et al. 2002), and habitat loss or degradation (Fischer and Lindenmayer 2007). In any habitat where interaction networks are simplified, there may be reductions in ecosystem functioning (Dobson et al. 2006, Jonsson et al. 2012) and hence in the provisioning of services. Habitat loss and landscape simplification drive biodiversity loss that in turn drives declines in ecosystem processes and functionality (Clergue et al. 2005, Tscharntke et al. 2005, Fischer and Lindenmayer 2007, Philpott et al. 2009).

In contrast, some agroecosystems harbor high levels of biodiversity and may act as refuges for biological diversity that can provide ecosystem services such as biological pest control and pollination (Perfecto et al. 1996, Moguel and Toledo 1999, Tscharntke et al. 2005, Jose 2009, Power 2010, Vandermeer et al. 2010). Different taxa vary in response to increases in tree diversity, canopy shade, and decreased agrochemical use (Moguel and Toledo 1999, Mas and Dietsch 2003, García Estrada et al. 2006, Gagic et al. 2012); thus, some taxa may be more sensitive to agricultural landscape changes and act as indicators of habitat simplification (e.g. Pocock and Jennings 2008, De la Mora and Philpott 2010). There are now numerous examples of increases in ecosystem services provided in less intensive agricultural systems, such as shaded coffee, compared with more intensive farms (e.g. Jha et al. 2014). Thus, we must focus on understanding how to promote less intensive agricultural production in order to prevent the increase of insect pests, reduced pollination, and

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loss of other ecological services (Kruess and Tscharntke 1994, Steffan-Dewenter 2002, Jha and Vandermeer 2010). Agricultural intensification and habitat complexity may strongly affect host–parasitoid interactions (Wilkinson and Feener 2007, 2012; Visser et al. 2009; Jonsson et al. 2012). Natural enemies, especially the parasitic Hymenoptera, play an important role in pest regulation (Rodríguez and Hawkins 2000, Varone and Briano 2009), and parasitoids and parasitism are affected by local habitat changes and changes at the landscape level (Klein et al. 2002, Fischer and Lindenmayer 2007). In addition, hymenopteran parasitoids are sensitive to agrochemical use and thus examining different host–parasitoid interactions where agrochemical use varies is necessary.

At the habitat level, two factors are important when parasites search for potential hosts: habitat preference (Townes 1960, Quilici and Rousse 2012, Mathis and Philpott 2012) and habitat complexity (Tylianakis et al. 2005, 2007; Wilkinson and Feener 2007, 2012; Vásquez-Ordóñez et al. 2012). Different habitat types vary spatially and temporally in terms of microclimate (Hsieh and Perfecto 2012), abundance and density of host colonies (Henne et al. 2008), and habitat complexity, each of which may promote greater diversity of parasitoids (Steffan-Dewenter 2002, Sperber et al. 2004, Hsieh and Perfecto 2012). For example, parasitism rate on immature stages of the ectatommine ant *Ectatomma ruidum* (Roger) by eucharitid wasps is higher in more complex habitats (woodlands) than in simple habitats (grasslands) that differ in vegetation composition and structure (Vásquez-Ordóñez et al. 2012). Moreover, agricultural intensification simplifies food web complexity and may affect host–parasitoid relationships (Jonsson et al. 2012). At the landscape level, other factors such as distance from forest habitat, hedgerows, or wooded fields may influence parasitism rate (Marino and Landis 1996, Klein et al. 2006), but landscape features are not always important for parasitism (e.g., Coudrain et al. 2013). In addition, agricultural matrix composition may alter host–parasitoid dynamics (Cronin 2007, Monmany and Aide 2009, Macfadyen and Muller 2013). In particular, landscapes with low habitat complexity may have lower diversity of natural enemies and therefore lower complementarity between natural enemies, which thereby alters ecological processes, and interactions (Menalled et al. 1999, Steffan-Dewenter 2002, Wilby and Thomas 2002, Jonsson et al. 2012).

In coffee and cacao agroecosystems, parasitism of ants may differ with agricultural management type (De la Mora and Philpott 2010) and with vegetation complexity (Vásquez-Ordóñez et al. 2012), but little attention has been given to differences in agroecosystems depending on landscape context. A study in Chiapas, Mexico, showed that the percentage of parasitism in ants is higher in primary forest than in different coffee management systems (De la Mora and Philpott 2010). Yet no studies have examined the relative importance of local and landscape drivers of ant parasitism in coffee agroecosystems. This interaction is important to investigate given the role of ants as biological control agents and predators in coffee agroecosystems

(Ibarra-Núñez et al. 2001, Philpott and Armbrecht 2006, Lachaud and Pérez-Lachaud 2009). Ants are also indicators of habitat quality (Andersen et al. 2002, Bution et al. 2010), and are sensitive to landscape fragmentation (Perfecto and Vandermeer 2002, Armbrecht and Perfecto 2003, Paolucci et al. 2012, De la Mora et al. 2013). Therefore, tropical agroforestry systems are an ideal system to study how both local and landscape changes influence ant parasitism with potential impacts for natural crop pest control.

Ants are parasitized by several organisms including eucharitid wasps (Hymenoptera: Chalcidoidea) (Johnson 1988, Heraty 1994, Lachaud and Pérez-Lachaud 2012), and some species of Eucharitidae have been considered for biological control of pest-ant species (Johnson 1988, Heraty 1994, Varone and Briano 2009, Lachaud and Pérez-Lachaud 2012). However, for predatory ants, such as genera of the subfamilies Ectatomminae and Ponerinae that sometimes prey on pest species in tropical agroecosystems, parasitism by eucharitids may interfere with biological control provided by ants (Pérez-Lachaud et al. 2006b, 2010; Lachaud and Pérez-Lachaud 2009). Parasitism of ants by eucharitids may be influenced by habitat type (Vásquez-Ordóñez et al. 2012), season (Pérez-Lachaud et al. 2006a), and host cocoon availability (Lachaud and Pérez-Lachaud 2009, Pérez-Lachaud et al. 2010). All of these factors may vary with changes in coffee management and in coffee landscapes. Here, we studied ant–parasitoid relationships in a coffee landscape to examine whether 1) habitat and season influence ant parasitism, 2) vegetation complexity and agrochemical use correlate with ant parasitism, and 3) specific local and landscape factors correlate with changes in ant parasitism.

Materials and Methods

Study Site, Local and Landscape Characteristics. This study was conducted in forty 20- by 20-m sites (30 coffee sites and 10 forest sites) within a coffee landscape in the Soconusco region of Chiapas, Mexico. The landscape is predominantly composed of coffee farms (93.7% of land cover) with scattered small forest fragments (6.3% of land area; Philpott et al. 2008b). The studied coffee sites can be further classified into management types categorized by Moguel and Toledo (1999): rustic and traditional polyculture (0.22% of the study area), traditional and commercial polyculture (36.91%), commercial polyculture (36.84%), commercial polyculture and shade monoculture (5.58%), shade monoculture (17.5%), and sun coffee (1.11%; Philpott et al. 2008b). Observations were done during the dry (February–March) and wet seasons (June–July) of 2010. All sites were located between 900–1,400 masl and averaged 4,000 mm rain per year. Coffee sites were organically or conventionally managed and also varied both in tree diversity and density and in canopy cover (De la Mora et al. 2013). The most common coffee shade trees in the study region include *Inga micheliana* Harms (Fabaceae), *Inga sapindoides* Willd (Fabaceae),

Trema micrantha (L.) Blume (Ulmaceae), and *Alchornea latifolia* Swartz (Euphorbiaceae).

The local and landscape factors of each site were characterized. At the local scale, site characteristics were examined, and farmers were interviewed regarding agrochemical use. Thirteen local factors were included: elevation, humus mass, tree circumference, tree height, percent canopy cover, richness of shade trees, density of shade trees, number of rotten logs, coffee plant density, and use of pesticides, herbicides, fertilizers, and fungicides (De la Mora et al. 2013). Seven landscape variables were studied including distance to the nearest forest edge, the area of forest within 50, 200, and 500 m of study sites, and the area of rustic coffee within 50, 200, and 500 m of study sites as determined with ArcGIS (Philpott et al. 2008b, De la Mora et al. 2013). To summarize vegetation and agrochemical use, two indices were created: 1) a vegetation complexity index (VCI) and 2) an agrochemical index (AI; Philpott et al. 2008a, De la Mora et al. 2013). Both indices range from 0 (low vegetation complexity or agrochemical use) to 1 (high vegetation complexity or agrochemical use). VCI values were used to classify coffee sites into high-shade coffee (13 sites with VCI between 0.37–0.609) and low-shade coffee (17 sites with VCI between 0.029–0.35).

Ant and Parasitoid Sampling. Within each site, rotten logs were sampled to find ants and their parasitoids. The subfamilies Formicinae (genus *Camponotus* only), Ponerinae, and Ectatomminae were studied, and they were chosen because these ants have pupae protected by a cocoon that is spun by the larvae prior to pupation (Wheeler 1915), and because ants with cocoons are the only potential hosts for parasitoids within the subfamily Eucharitinae (Heraty et al. 2004, Murray et al. 2013). Rotten log pieces were carefully opened with an ax and knives to facilitate collection of cocoons. All of the cocoons encountered for species of Ponerinae, Ectatomminae, and *Camponotus* in each log sampled were collected, counted, and placed into plastic cups covered with mesh. A representative sample of workers (10–15 individuals per colony) was collected and stored in vials with alcohol and later identified according to Bolton (1994) and Longino (2011). Parasitism was examined by first waiting for parasitoid emergence, and second, by dissecting ant cocoons. Cocoons were checked daily for 10 d for emergence of parasitoids. After 10 d, the remaining cocoons were dissected to determine the total parasitism rate in each colony. Voucher specimens of ants were deposited in the Entomology Collection at El Colegio de la Frontera Sur in Tapachula, Chiapas, Mexico, and parasitoids were deposited in the Department of Entomology at the University of California, Riverside.

Data Analysis. Parasitism was examined with several metrics. First, presence or absence of parasitism was used. Second, the proportion of species parasitized (in other words, the number of species in a plot from which parasitism was detected divided by the total number of species encountered in that plot) was used. Third, the proportion of cocoons parasitized for

common genera and common species (nested within the common genera) was examined. Common genera and species were defined as those that were found from at least two colonies in each of the three habitat types sampled (forest, high-shade coffee, low-shade coffee) and from at least two colonies in each season sampled (wet, dry). The different measures were examined to assess differences in parasitism with local and landscape context at both the community (e.g., more or fewer species parasitized, higher parasitism of ants in a single genus) and population levels (e.g., higher proportion of pupae of a single species parasitized).

To examine whether habitat and season influence ant parasitism, generalized linear mixed models (GLMMs) with "glmer" in the "lme4" package in R were used (R Development Core Team 2012). GLMMs allow analysis with count or proportional responses (Bolker et al. 2008) and the dependent variables included were presence of parasitism, proportion of species parasitized, proportion of cocoons of common genera (*Gnamptogenys*, *Odontomachus*, *Pachycondyla*) parasitized, and proportion of cocoons of common species (*Gnamptogenys sulcata* (F. Smith), *Odontomachus chelifer* (Latreille)) parasitized in each site during each season. Habitat type (forest, high-shade coffee, low-shade coffee), season (wet, dry), and the interaction between habitat and season were included as fixed effects, the number of cocoons (total, or for each genus or species) was included as a random effect, and the binomial error distribution with the logit link was used. For all dependent variables that were proportions, the "cbind" function was used with proportion parasitized and proportion not parasitized as input variables.

To examine whether vegetation complexity and agrochemical use correlate with parasitism, general linear models (GLM) in R were used (R Development Core Team 2012). The dependent variables included were presence of parasitism, proportion of species parasitized, and proportion of cocoons of *Gnamptogenys*, *Odontomachus*, *Pachycondyla*, *G. sulcata*, and *O. chelifer* that were parasitized in each site. For each dependent variable, eight different predictive models were tested including—1) VCI as a linear predictor, 2) VCI as a quadratic predictor, 3) AI as a linear predictor, 4) AI as a quadratic predictor, 5) both VCI and AI as linear predictors, 6) VCI as a linear predictor and AI as a quadratic predictor, 7) VCI as a quadratic predictor and AI as a linear predictor, and 8) both VCI and AI as quadratic predictors. All models were tested with and without the number of cocoons (overall, or for each genus or species tested) as an additional explanatory variable for a total of 16 total models tested for each dependent variable. To select the best model among the 16 possible models, the Akaike's information criterion (AIC) computed with the "mass" package (Venables and Ripley 2002). For each GLM, a binomial error distribution with logit link was used, and for all dependent variables that were proportions, the "cbind" function was used with proportion parasitized and proportion not parasitized as input.

Table 1. Ant morphospecies in the subfamilies Ectatomminae, Formicinae, and Ponerinae examined for eucharitid parasitoids in forest and coffee habitats in Chiapas, Mexico

	No. cocoons collected			Parasitized cocoons (%)[b]		
Morphospecies	F	HSC	LSC	F	HSC	LSC
Camponotus atriceps (F. Smith)	0	153	88	NA	7.19	0
Camponotus striatus (F. Smith)	29	0	0	0	NA	NA
Gnamptogenys sp. 1	79	184	0	16.46	0	NA
Gnamptogenys striatula Mayr[a]	66	58	211	0	0	0
Gnamptogenys sulcata (F. Smith)[a]	135	871	425	1.48	1.15	0.71
Gnamptogenys wheeleri (Santschi)	0	81	13	NA	0	0
Leptogenys sp. 1[a]	13	7	3	0	0	0
Odontomachus chelifer (Latreille)[a]	11	43	421	0	6.98	3.33
Odontomachus meinerti Forel	0	29	0	NA	6.90	NA
Pachycondyla apicalis (Latreille)[a]	21	42	39	0	0	0
Pachycondyla cf. *cognata* (Emery)[a]	8	173	442	0	0	0
Pachycondyla harpax (F.)	41	0	49	0	NA	0
Pachycondyla impressa (Roger)[a]	32	79	18	6.25	0	0
Pachycondyla sp. 1	0	7	0	NA	0	NA
Platythyrea punctata (F. Smith)	0	12	13	NA	0	0
Typhlomyrmex rogenhoferi Mayr	0	105	0	NA	0	NA

Data show total numbers of cocoons, and the proportion of parasitized cocoons for 10 forest (F) sites, 13 high-shade coffee sites (HSC), and 17 low-shade coffee sites (LSC) sampled during the dry and the rainy season of 2010.

Morphospecies in bold print were parasitized.

NA indicates that there were no cocoons in that habitat that could have been parasitized.

[a] Species with cocoons found in all three habitats.

[b] Calculated based on total number of parasitized and unparasitized cocoons across all sites sampled.

To examine whether specific local and landscape factors correlate with changes in ant parasitism, conditional inference trees were created with the "party" package in R (Hothorn et al. 2006, Strobl et al. 2009). The dependent variables included were presence of parasitism, proportion of species parasitized, and proportion of cocoons of *Gnamptogenys*, *Odontomachus*, *Pachycondyla*, *G. sulcata*, and *O. chelifer* that were parasitized in each site. The predictor variables included the 13 local and 7 regional factors measured for each site, plus the number of cocoons and number of ant colonies (overall or for individual genera or species examined).

Because some study plots were located within 250 m of one another, the degree of spatial autocorrelation in the residuals of the best-fit GLM models and conditional inference trees was tested using—1) spatial correlograms (with the "ncf" package in R) and 2) the Moran's test for spatial autocorrelation using a spatial weights matrix with the "spdep" package in R (Bivand et al. 2012, R Development Core Team 2012). For the correlograms, 100 permutations were computed using the *resamp* argument in the *correlog* function to examine the distance, if any, at which variables were spatially autocorrelated. For the calculation of Moran's I, the nearest neighbor distances were included as the metric, and the permutation test option was used. In those analyses that revealed significant spatial autocorrelation, longitude and latitude were included as additional predictor variables, but they did not improve the fit of any of the tested models, and were removed from the models presented in the results (Supp Table 1 [online only]).

Results

Across all sites sampled, 4,006 cocoons from 16 ant species belonging to the subfamilies Ponerinae (9 species), Ectatomminae (5 species), and Formicinae (2 species) were collected (Table 1). Seven of the 16 species (43.8% of species) were parasitized. *G. sulcata* was parasitized in all three habitats and was attacked by at least three different parasitoid species. But overall parasitism of *G. sulcata* was low (1.05% of cocoons were parasitized; Table 1). All parasitoids we found were Eucharitidae (E. A. Murray and J. M. Heraty, personal communication) and belonged to at least three species in the genus *Kapala* Cameron and to one new, undescribed species in the genus *Obeza* Heraty (Supp Table 2 [online only]). *Camponotus atriceps* (F. Smith) was parasitized by *Obeza* n. sp.; *Gnamptogenys* sp. 1 was parasitized by *Kapala izapa* (Carmichael) and *Kapala* sp.; *G. sulcata* was parasitized by *Kapala* nr. *sulcifacies*, *K. izapa*, and *Kapala* sp.; and *O. chelifer*, *Pachycondyla harpax* (F.), and *Pachycondyla impressa* (Roger) were parasitized by *Kapala* nr. *sulcifacies* (Supp Table 2 [online only]). *Odontomachus meinerti* Forel was parasitized by an eucharitid species that could not be determined to species because only juvenile stages were found.

Parasitism of ants by eucharitid wasps did not differ with habitat type, but parasitism of ants in one genus (*Gnamptogenys*) and one species within that genus (*G. sulcata*) varied with season (Table 2). Presence of parasitism, the proportion of parasitized species, and proportion of parasitized cocoons of *Gnamptogenys*, *Odontomachus*, *Pachycondyla*, *G. sulcata*, and *O. chelifer* did not differ in forest, high-shade, or low-shade coffee, and no parasitism metrics demonstrated a significant habitat by season interaction (Table 2). Parasitism of *Gnamptogenys* cocoons was 1.5 times higher in the dry season than in the wet season and parasitism of *G. sulcata* was >10 times higher in the dry season than in the wet season (Table 2). Presence of parasitism, the proportion of parasitized species, and proportion of parasitized cocoons of *Odontomachus*, *Pachycondyla*, and *O. chelifer* did not differ with season.

Table 2. Results of a generalized linear mixed model testing for differences in ant parasitism by Eucharitidae in forest, high-, and low-shade coffee agroecosystems and in the wet and dry season in coffee landscapes in Chiapas, Mexico

	Habitat			Season		N	F-value		
	Forest	High-shade	Low-shade	Wet	Dry		Habitat	Season	Habitat × Season
Presence of parasitism[a]	0.3 ± 0.153	0.368 ± 0.114	0.176 ± 0.095	0.281 ± 0.081	0.286 ± 0.125	46	0.446	0.016	0.005
Prop. of species parasitized	0.25 ± 0.134	0.232 ± 0.086	0.078 ± 0.043	0.133 ± 0.043	0.286 ± 0.125	46	0.450	0.139	0.009
Prop. of *Gnamptogenys* cocoons parasitized	0.043 ± 0.039	0.017 ± 0.015	0.002 ± 0.002	0.015 ± 0.014	0.024 ± 0.019	27	0.523	1.424*	0.453
Prop. of *Odontomachus* cocoons parasitized	0 ± 0	0.055 ± 0.021	0.023 ± 0.016	0.035 ± 0.014	0.016 ± 0.016	12	0.673	0.510	<0.001
Prop. of *Pachycondyla* cocoons parasitized	0.018 ± 0.018	0 ± 0	0 ± 0	0.006 ± 0.006	0 ± 0	20	<0.001	<0.001	<0.001
Prop. of *G. sulcata* cocoons parasitized	0.007 ± 0.007	0.025 ± 0.021	0.003 ± 0.003	0.002 ± 0.002	0.03 ± 0.023	17	0.762	6.726*	<0.001
Prop. of *O. chelifer* cocoons parasitized	0 ± 0	0.048 ± 0.027	0.023 ± 0.016	0.026 ± 0.014	0.024 ± 0.024	11	0.402	0.297	<0.001

[a] Presence or absence in individual sites was coded as 0 or 1, and the mean across all sites was calculated, and reported here.
* $P < 0.05$.

Table 3. Results of generalized linear models testing relationships between dependent variables, the vegetation complexity index (VCI), agrochemical index (AI), and the number of ant cocoons found in a site

Dependent variable	Best Model	VCI	VCI^2	AI	AI^2	Number of cocoons
Presence of parasitism	AI^2 + number of cocoons	NA	NA	0.329	<0.001	0.025
Prop. of species parasitized	AI^2	NA	NA	0.376	0.002	NA
Prop. of *Gnamptogenys* cocoons parasitized	VCI + AI^2 + number of *Gnamptogenys* cocoons	<0.001	NA	0.237	<0.001	<0.001
Prop. of *Odontomachus* cocoons parasitized	AI^2	NA	NA	0.641	0.001	NA
Prop. of *Pachycondyla* cocoons parasitized	VCI^2	0.038	<0.001	NA	NA	NA
Prop. of *G. sulcata* cocoons parasitized	AI^2	NA	NA	0.087	<0.001	NA
Prop. of *O. chelifer* cocoons parasitized	AI^2	NA	NA	0.313	0.003	NA

NA indicates that variable was not included in the best model.
Numbers show *P*-values for predictor variables as determined with generalized linear mixed models.

Agrochemical use (AI), vegetation complexity (VCI), and the number of ant cocoons were all frequently included in models predicting ant parasitism (Table 3). Presence of parasitism was highest at low and high AI values and also increased with increases in the number of ant cocoons (Table 3; Fig. 1). The proportion of parasitized species and the proportions of parasitized *Odontomachus*, *G. sulcata*, and *O. chelifer* cocoons were high at both low and high AI values (Table 3; Figs. 1 and 2). *Gnamptogenys* parasitism increased with VCI, decreased with number of cocoons, and was high with low and high AI values (Table 3; Fig. 2). Finally, parasitism of *Pachycondyla* cocoons increased with VCI (Table 3; Fig. 2).

The conditional inference tree analyses revealed one local, two landscape, and one ant density predictor of parasitism. The presence of parasitism increased in sites with more rustic coffee area within 200 m and with more cocoons (Fig. 3a). The proportion of parasitized species increased in sites with more forest area within 200 m and with more cocoons (Fig. 3b). The proportion of parasitized *Gnamptogenys* cocoons increased in sites with higher humus mass (Fig. 3c). The proportion of parasitized *Odontomachus*, *Pachycondyla*, *G. sulcata*, and *O. chelifer* cocoons did not correlate with any local, landscape, or ant density variable.

Discussion

Seven ant species found were parasitized by Eucharitidae parasitoids and at least seven previously unknown host–parasitoid relationships were recorded: *C. atriceps* parasitized by *Obeza* n. sp., *Gnamptogenys* sp. 1 parasitized by *K. izapa*, *Gnamptogenys* sp. 1 parasitized by *Kapala* sp., *G. sulcata* parasitized by *Kapala* nr. *sulcifacies*, *O. chelifer* parasitized by *Kapala* nr. *sulcifacies*, *P. harpax* parasitized by *Kapala* nr. *sulcifacies*, and *P. impressa* parasitized by *Kapala* nr. *sulcifacies*. One other association detected, *G. sulcata* parasitized by *K. izapa*, was previously reported (Pérez-Lachaud et al. 2006b). Two final associations, *G. sulcata* parasitized by *Kapala* sp. and *O. meinerti* parasitized by an undetermined eucharitid species, probably correspond to previous reports involving *Kapala iridicolor* and *Kapala* sp., respectively (Pérez-Lachaud et al. 2006b, De la Mora and Philpott 2010). Most of the parasitized ant species were in the Ponerinae and Ectatomminae subfamilies, but we also report the first case of parasitism of *C. atriceps* (Formicinae subfamily) by a parasitoid in the genus *Obeza* Heraty. This is the second report of the genus *Obeza* attacking a *Camponotus* species for the state of Chiapas (see Pérez-Lachaud and Lachaud 2014). *K. izapa* parasitized two species of *Gnamptogenys* in our study sites and thus has at least three
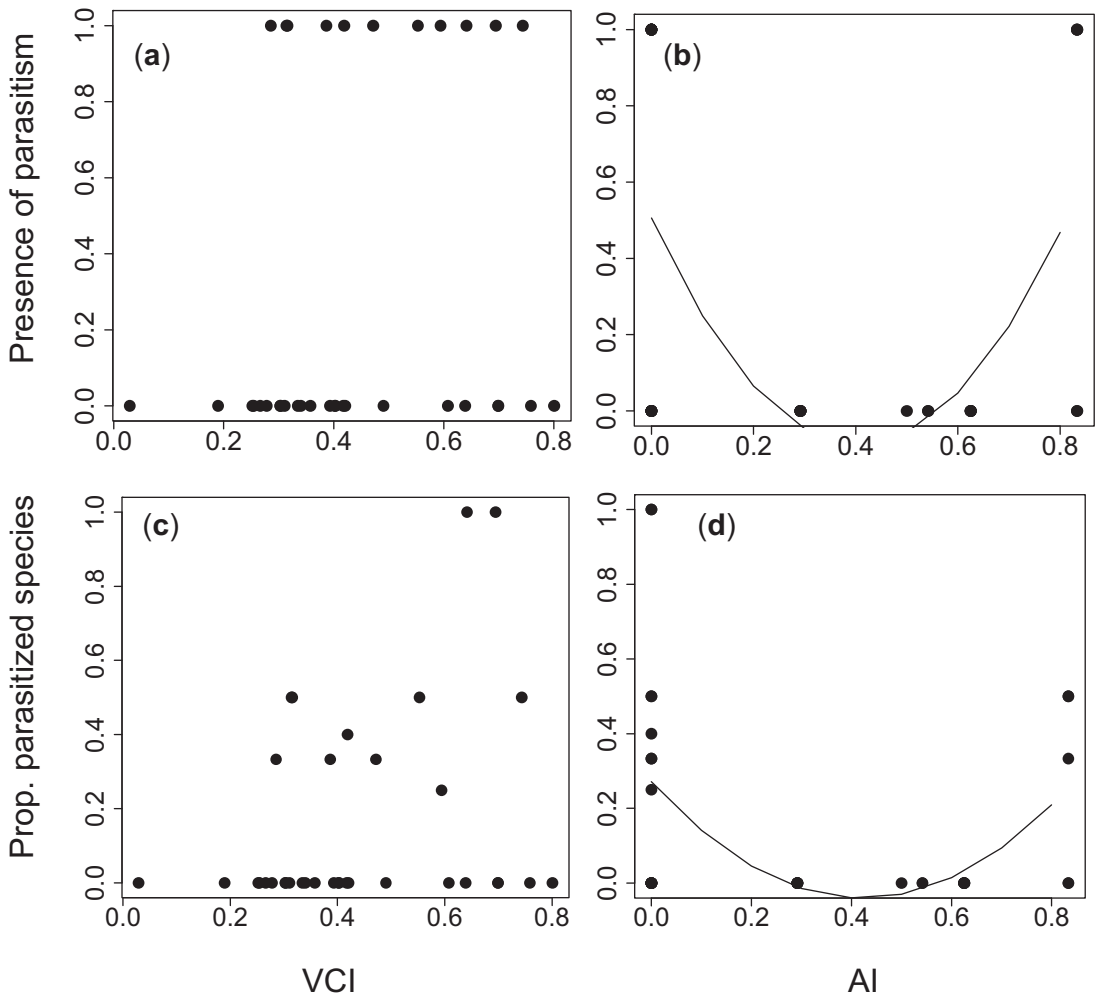
Fig. 1. Relationships between presence of parasitism of ants by eucharitid parasitoids (a, b) and proportion of species parasitized by eucharitids (c, d) and vegetation complexity and agrochemical use in coffee landscapes.

potential hosts in this genus (see Pérez-Lachaud et al. 2006b). *Kapala* nr. *sulcifacies* parasitized four species of ants from three different genera (Supp Table 2 [online only]). One ant species (*G. sulcata*) was parasitized by more than one *Kapala* species (Supp Table 2 [online only]). Other studies document that ant species can be parasitized by multiple species of parasitoids (Pérez-Lachaud et al. 2006b, Torréns 2013), sometimes as multiparasitism where the same individual host is parasitized by multiple species of parasitoids (Pérez-Lachaud et al. 2006a). In addition, several parasitoid species can parasitize multiple species of host ants (Pérez-Lachaud et al. 2006b, Lachaud and Pérez-Lachaud 2012) as we found for *K. izapa* and *Kapala* nr. *sulcifacies*. Although some ant species collected were not parasitized, some of them (*Gnamptogenys striatula* Mayr, *Pachycondyla apicalis* (Latreille), and *Typhlomyrmex rogenhoferi* Mayr) are known hosts of Eucharitidae parasitoids (Pérez-Lachaud et al. 2006b, De la Mora and Philpott 2010). Unfortunately, many specific

ant–parasitoid relationships could not be determined at the species level, as many parasitoids collected as larvae or prepupae could not be identified.

Parasitism and Local Habitat and Vegetation Features. One study objective was to study whether ant parasitism by Eucharitidae wasps varied in different habitats, and whether parasitism varied with vegetation features and agrochemical use in coffee farms and forests. Presence of parasitism, the proportion of species parasitized, and the proportion of parasitized cocoons of common genera and species examined did not differ with habitat type. This may be because there was high within-habitat variability in vegetation characteristics measured in high-shade and low-shade coffee sites, and VCI may be a better measure of the specific vegetation changes in study sites. In fact, parasitism of *Gnamptogenys* and *Pachycondyla* (the genera with most numerous colonies and cocoons in the study sites) increased as vegetation complexity increased. It may have been difficult to detect differences in parasitism for
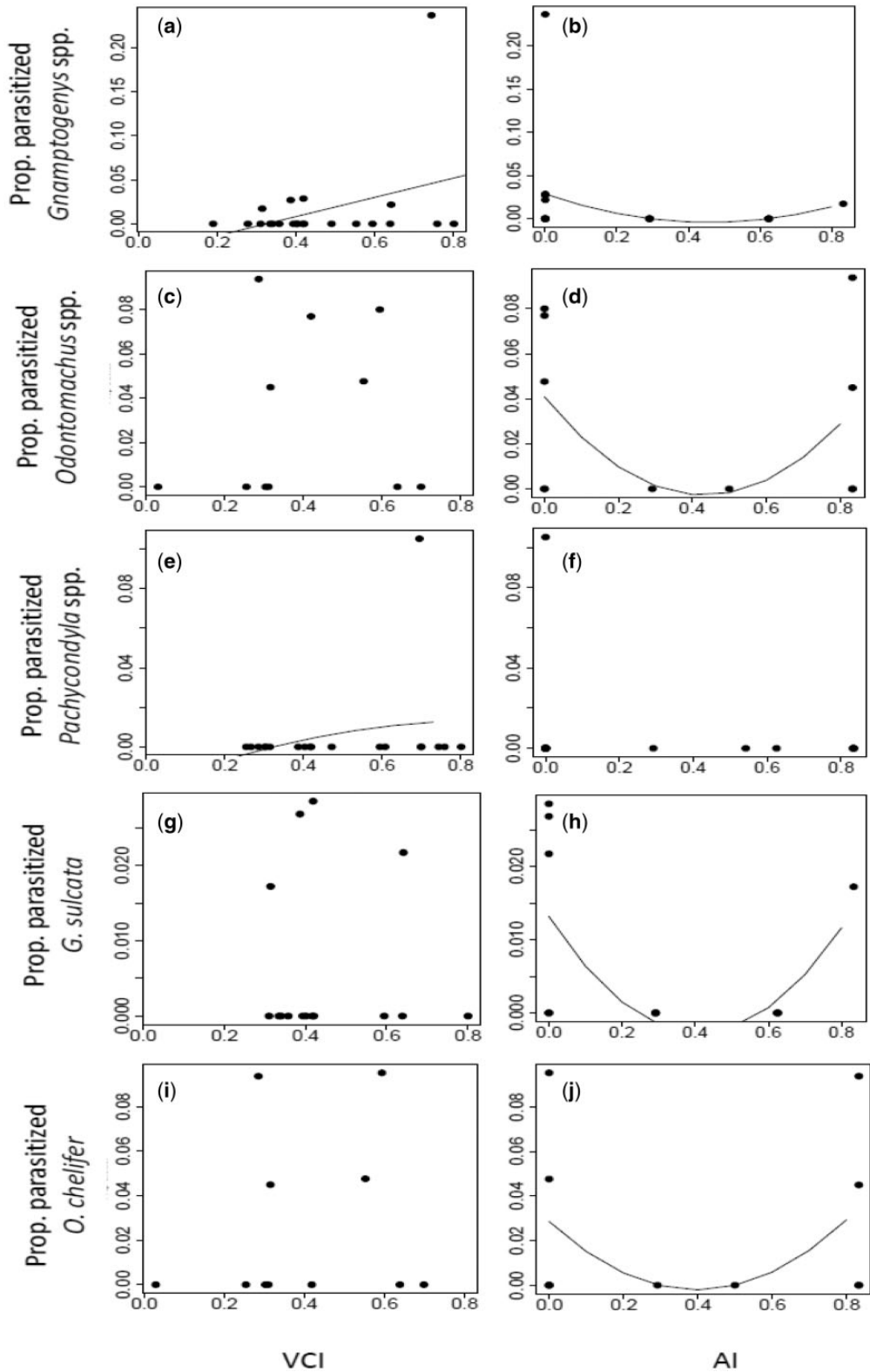
Fig. 2. Relationship between proportion of parasitized cocoons of *Gnamptogenys* (a, b), *Odontomachus* (c, d), *Pachycondyla* (e, f), *G. sulcata* (g, h), and *O. chelifer* (i, j) and vegetation complexity (VCI) and agrochemical use (AI) in coffee landscapes.
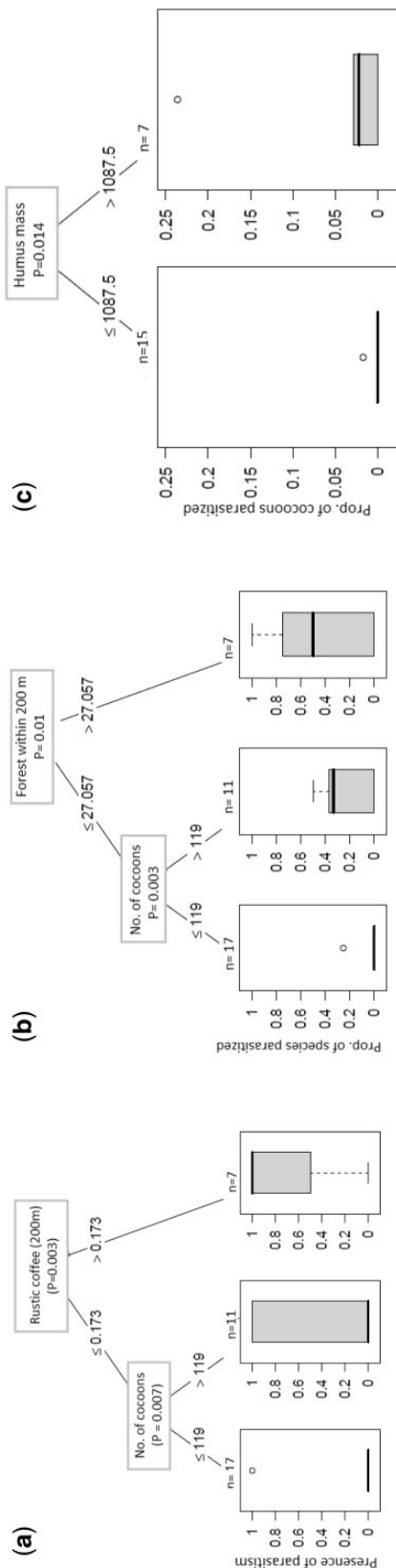
Fig. 3. Conditional inference trees testing relationships between 13 local and 7 regional factors and: (a) presence of parasitism, (b) proportion of parasitized ant species, and (c) proportion of parasitized *Gnamptogenys* cocoons in coffee landscapes. Predictor variables in boxes are ranked (top, highest correlation with dependent variable). *P*-values indicate the significance at 95% of confidence in the relationship tested. Box plots include the inner quartiles (grey box), the median values (solid black line), and 1.5 × the inner quartiles (error bars) of cocoons parasitized associated with each string of predictor variables. Sample sizes at each terminal node show the number of sites in that box plot.

Odontomachus and common species due to low numbers of cocoons collected. Habitat type may affect ant parasitism (De la Mora and Philpott 2010, Vásquez-Ordoñez et al. 2012). Adult parasitoids rely on nonhost food sources in agroecosystems (e.g., honeydew, nectar, or pollen), and increases in vegetation complexity may increase resource availability within agricultural habitats increasing parasitoid abundance and richness (Landis et al. 2000, Sperber et al. 2004). However, neither presence of parasitism nor the proportion of ant species that were parasitized shifted with habitat type or VCI. Different ant species or genera (or their parasitoids) respond to changes in habitat or vegetation in different ways, and examining species together may have masked taxonomic variability in response to habitat or vegetation changes.

We found high presence of parasitism, high proportion of parasitized species, and high proportions of parasitized *Gnamptogenys*, *Odontomachus*, *G. sulcata*, and *O. chelifer* cocoons in sites with low and high agrochemical use. Agrochemical use can more strongly affect parasitism than changes in floral resources or host populations (Jonsson et al. 2012). In sites with low agrochemical use, high parasitism may have resulted from high parasitoid abundance and diversity. Abundance and richness of parasitoids is negatively affected by nematocide and insecticide application (Matlock and de la Cruz 2002), and use of the insecticide endosulfan (i.e., brand name Thiodan) is common in the study region (Damon 2000). Almost all of the sites with zero agrochemical use were forests, and thus, some other feature of the forests, such as increases in resources, not measured in this study may have contributed to the observed pattern.

Explaining increases in parasitism in sites with high agrochemical use is less intuitive, but may relate to changes in understory vegetation or weed cover with herbicide application, impacts of fertilizers on ant species richness, influences of pesticides on insect behavior, or increases in presence of trees with extrafloral nectaries in sites with high agrochemical use. First, herbaceous vegetation strongly impacts parasitoid–ant interactions (Clausen 1940) and regular use of herbicides in some study sites may have affected parasitism. Composition of herbaceous plants (e.g., weeds) may differ in sites with high and low herbicide use (A. De la Mora, personal observation.). Although weed cover was not quantified in this study, field observations indicate that *Impatiens* spp. are the most common weed species in high agrochemical sites whereas *Lantana* spp., *Ipomea* spp., and *Vernonia* spp., as well as other plants in the family Asteraceae and Gramineae, are more common in low agrochemical sites. Changes in herbaceous plant composition may influence both ant foraging patterns (Lachaud and Pérez-Lachaud 2009, Gibb and Parr 2010) and eucharitid oviposition (Johnson 1988, Pérez-Lachaud et al. 2006b). All eucharitid species oviposit away from the host in or on plant tissues (Clausen 1940). For example, some *Kapala* species oviposit on leaves, flower buds, or on seed receptacles (Clausen 1940, 1941; Wojcik 1989; Pérez-Lachaud et al. 2006b; Lachaud and Pérez-Lachaud 2009), and herbicide use

may alter oviposition site availability for and parasitism by *Kapala*. Second, agrochemical use, and specifically fertilizer use, might alter ant species richness, with subsequent impacts on parasitism. Increased fertilizer use correlates with decreased species richness of ants that nest in rotting logs (e.g., *Pachycondyla*, *Gnamptogenys*, and *Odontomachus* species; De la Mora et al. 2013). Such changes in species richness and abundance of certain ant species in different sites may have influenced parasitism. For example, in agricultural landscapes in Ecuador, increases in agricultural intensification resulted in increases in hymenopteran parasitoid diversity, reduced hymenopteran host diversity, increased specificity of observed parasitism for some parasitoids, and reduced attacks on alternative hosts (Tylianakis et al. 2007). In our system, increases in agrochemical use may have reduced ant diversity, while at the same time limiting the number of host species available to parasitoids, potentially resulting in higher parasitism for species present. Third, some parasitoids benefit from extrafloral nectaries on shade trees within coffee agroecosystems (Rezende et al. 2014), and presence of extrafloral nectaries may covary with agrochemical use. *Inga* spp. trees, which contain extrafloral nectaries, are common shade trees in coffee farms studied, and most trees (∼70%) in high agrochemical sites were *Inga* trees. Sites with low agrochemical use have fewer *Inga* trees (∼57% of trees). In the study sites, *Kapala* spp. parasitoids visit extrafloral nectaries on *Inga vera* Wild (M. E. Jiménez-Soto, personal communication). Increases in nectar resources may have compensated for the negative impacts of agrochemicals in high agrochemical sites. Finally, all of the high agrochemical sites with high parasitism were found in a single, large farm (Finca Hamburgo). Thus, some farm-specific feature such as management or history of chemical use may have influenced the observed results.

Parasitism and Season. For most parasitism metrics examined, parasitism did not differ in the wet and dry season. However, parasitism of *Gnamptogenys* and *G. sulcata* were higher in the dry season than in the wet season. Seasonal changes in parasitism may relate to changes in ant reproductive cycles or brood production (see Lachaud and Pérez-Lachaud 2009, Pérez-Lachaud et al. 2010). For instance, some ant species susceptible to eucharitid parasitism, such as *Ectatomma ruidum*, produce more cocoons in the wet season, when they also experience higher rates of parasitism by *K. izapa* and *K. iridicolor*, and thus some eucharitid parasitoids demonstrate positive density dependence (Lachaud and Pérez-Lachaud 2009). Yet, we did not find positive density dependence for *Gnamptogenys* parasitism. *Gnamptogenys* parasitism decreased with increases in *Gnamptogenys* cocoons, and *G. sulcata* parasitism did not vary with changes in *G. sulcata* cocoon numbers. Seasonal changes in food and nesting resources for ants and parasitoids in different seasons may alter ant–parasitoid interactions (Clausen 1940, 1941). Shifts in parasitism with season are often due to changes in physical characteristics of sampled habitats (Tylianakis et al. 2005). Additionally, flowering of certain common herbaceous weeds, such as *Melampodium*

divaricatum (Asteraceae), a known oviposition site for *K. iridicolor* (Pérez-Lachaud et al. 2006b), occurs in the dry season (A. De la Mora, personal observation), potentially explaining increased parasitism rates for *Gnamptogenys* spp. and *G. sulcata* during the dry season. Pérez-Lachaud et al. (2006a) suggest that presence or absence of certain herbaceous plants throughout the year may affect the spatial distribution of eucharitid wasps that parasitize *Ectatomma tuberculatum*. Oviposition sites are an important factor determining parasitism of ants by eucharitids. Adult wasps are not highly mobile and rely on foraging ants to pick up a planidium and transport it to the nest. At the same time, increases in ant foraging activity in patches of vegetation with high resources may facilitate parasitism success (Clausen 1940, 1941; Johnson 1988; Wojcik 1989). Additionally, abundance of eucharitid predators may shift in the wet and dry season, thereby influencing eucharitid abundance. Eucharitids may be trapped in spider webs, and changes in web-building spider abundance in different seasons might influence predation risk for the parasitoids. However, available data from the study sites indicates that web-building spider abundance is higher in the dry season (Pinkus et al. 2006), which would presumably lower eucharitid abundance and result in lower ant parasitism. A lack of seasonal differences in parasitism for other genera and species may have been hindered by low numbers of colonies and specifically parasitized colonies.

Parasitism and Local and Landscape Factors. A final study objective was to determine relationships between parasitism of ants by eucharitids and local and landscape features of coffee landscapes. Presence of parasitism and the proportion of species parasitized were each correlated with one landscape factor and with the number of ant cocoons found in those study sites. The presence of parasitized cocoons increased with rustic coffee area within 200 m and the proportion of parasitized ant species increased with forest cover within 200 m. Landscape composition and complexity are often important for hymenopteran parasitoid abundance and parasitism (e.g., Marino and Landis 1996; Thies et al. 2003; Tylianakis et al. 2005, 2007; but see Menalled et al. 1999). Greater vegetation complexity in a landscape, such as that found in forest and rustic coffee sites, can promote mobility of Hymenoptera across habitats (Tylianakis et al. 2005) and can act as sources for other nearby areas. In addition, increases in habitat complexity at the landscape scale result in increased parasitoid diversity (Sperber et al. 2004, Menalled et al. 1999), and parasitoid diversity, in turn, may relate to higher complementarity and parasitism (Wilby and Thomas 2002). Increases in the amount of noncrop (e.g., forest) habitat and of complex habitats (e.g., rustic coffee) in the landscape may provide alternative hosts and other resources for parasitoids, leading to higher parasitoid abundance and parasitism rates (Thies et al. 2003). Landscape changes at the 200 m scale (and not other spatial scales examined) significantly predicted changes in parasitism. Different studies have documented differences in parasitoids and in parasitoid–host interactions, but no consensus yet exists

on which spatial scale results in maximum change in which system. Thies et al. (2003) examined the influence of noncrop habitat within 0.5–6 km on parasitism for different hymenopteran parasitoid species. They found that noncrop habitat influenced parasitism rate most highly at spatial scales of between 1–2 km (Thies et al. 2003). An additional study found that parasitoid diversity responded to changes in habitat composition at the 300-m scale, but did not address parasitism rates specifically (Bennett and Gratton 2012).

Gnamptogenys parasitism increased with increases in humus mass, a local change. Agricultural systems with less humus support fewer resources for ground-dwelling ant species and can lead to reductions in the abundance or richness of ants (Mertl et al. 2009). But supplementing litter and humus biomass will increase insect prey resources and thereby increase brood production for ground-dwelling ants (McGlynn et al. 2009, Shik and Kaspari 2010), which may in turn lead to increases in parasitism rate by these density-dependent parasitoids.

The local habitat and landscape predictors of ant parasitism by eucharitid parasitoids are not well studied. Here, both local and landscape complexity correlated with changes in ant parasitism. Overall, presence of parasitism in the landscape was influenced by the amount of rustic coffee and forest habitat nearby and parasitism of two abundant ant genera increased with local vegetation complexity. Presence of parasitism increased with increases in the number of cocoons, but no positive density dependence in parasitism of any ant species or genus examined was detected. Parasitism for *Gnamptogenys* and *G. sulcata* was higher in the dry season. Agrochemical use was both negatively and positively associated with parasitism for most common genera and species, but the reasons for these patterns remain somewhat elusive. Generally, better knowledge of the oviposition in host plants and the specificity of parasitoids to these hosts, could greatly enhance our understanding of host parasitism rates in this and other habitat types. Future studies on ant–parasitoid relationships should examine changes in availability of eucharitid oviposition sites and herbaceous vegetation in study sites, as well as changes in ant–parasitoid specificity, as these differences may explain the results observed in this study. Differences between ant parasitism in different locations within the landscape may have implications for other trophic interactions and ecosystem services in agricultural landscapes.

Supplementary Data

Supplementary data are available at *Economic Entomology* online.

Acknowledgments

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