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Local, landscape, and diversity drivers of predation services provided by ants in a coffee landscape in Chiapas, Mexico

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ABSTRACT

Agricultural management and the landscape surrounding farms impact biological diversity and ecosystem services, such as predation, in agroecosystems. Diversified coffee agroecosystems harbor biodiversity, and maintain ecosystem services, especially when in complex landscapes, and when diversity of organisms providing services is maintained. But few have examined whether biological diversity, per se, or the local and landscape habitat features are stronger drivers of the services provided. We studied the relationships between local characteristics associated with agricultural management (vegetation complexity and agrochemical use), landscape surroundings of farms, abundance and richness of ants, and predation services provided by ants in a tropical coffee landscape. Specifically, we tested whether: (1) ants remove prey items and prey removal differs in the wet and dry season, (2) ant prey removal differs in farms that vary in vegetation complexity and agrochemical use, (3) ant prey removal differs with changes in ant abundance and species richness, and (4) ant prey removal differs with changes in local and landscape characteristics. We established sites across a range of coffee management systems, at varying distances to forest fragments, and in forest fragments and examined prey removal by ants on the ground, coffee branches, and shade tree trunks in the wet and dry season. Prey removal did not differ with season. Prey removal on the ground increased within increases in ant abundance and richness, and number of hollow coffee twigs. Prey removal on coffee plants decreased with vegetation complexity, but increased with ant abundance and richness, coffee density (a local factor), and rustic coffee within 200 m (a landscape factor). Prey removal on trees declined with vegetation complexity, but increased with abundance and richness of ants. Characteristics of the ant community were consistent predictors of prey removal, whereas local and landscape habitat features were less important, and only three habitat features correlated with prey removal. Our results demonstrate the positive effects of ant diversity for predatory function, and that promoting pest control services within coffee agroecosystems may be best accomplished by manipulating ant abundance and richness, or vegetation factors that correlate with ants.

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1. Introduction

1.1. Biodiversity, agricultural intensification, and landscape change

Ecosystem services in biodiverse ecosystems may be more robust to disturbance in comparison to simplified landscapes such as those under agricultural production. However, the drivers of the maintenance of ecosystem services remain unclear. Few have examined whether biodiversity per se or local or landscape complexity are the drivers of ecosystem service maintenance

(Klein et al., 2002; Matson et al., 1997; Perfecto et al., 1997). An ideal setting to study the effect of intensification on ecosystem services is in agroecosystems ranging in management from diverse, complex systems to monocultures.

Agricultural intensification results in extensive, input dependent monocultures that simplify the agricultural environment, while aiming to increase agricultural profits (Bisseleua et al., 2009; Matson et al., 1997). This agricultural intensification process creates matrices of homogeneous monocultures with interspersed fragments of natural vegetation (Fahrig, 2003; Vandermeer and Perfecto, 2007). Agricultural intensification results in habitat loss, alteration of ecological communities and interactions (Fischer et al., 2006; Vandermeer et al., 2010) and also affects physical characteristics such as microclimate, structure, size, diversity, and

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distribution of native vegetation patches (Dauber et al., 2003; Fahrig, 2003; Tschardt et al., 2002). Changes in habitats, as well as landscape changes may significantly impact trophic interactions (Vandermeer and Carvajal, 2001). Our work aims to study the relationship between habitat and landscape modification, predator abundance and richness, and predation services in a coffee landscape.

1.2. Agricultural landscape change, biodiversity, and ecosystem services

Changes in agricultural landscapes result in biodiversity loss with implications for ecosystem services. Management intensification can alter the structure and complexity of trees in cropping systems as well as increased use of agrochemicals, and both changes can affect the potential for these systems to harbor biodiversity (De la Mora et al., 2013; Bisseleua et al., 2009; García Estrada et al., 2006; Klein et al., 2003; Moguel and Toledo, 1999). Transformation of complex agroecosystems to monocultures results in losses of bird, ant, bee, and bat diversity (García Estrada et al., 2006; Klein et al., 2002; Perfecto et al., 1997; Perfecto and Vandermeer, 2002; Philpott et al., 2008a). Such species losses can affect trophic interactions and food webs (Dauber et al., 2005; Klein et al., 2002; Perfecto and Vandermeer, 2006). With agricultural intensification, a loss of taxonomic or functional diversity, or complementarity of organisms within ecological networks can diminish the provisioning of ecosystem services such as pollination, predation, and parasitism needed in agroecosystems (Klein et al., 2002; Wilby and Thomas, 2002).

Yet conserving biodiversity in agricultural habitats promotes biological control (Fischer et al., 2006; Vandermeer et al., 2010). Habitat and landscape complexity and increases in species richness promote complex ecological networks (Dauber et al., 2003, 2005; Ibarra-Núñez, 1990; Moguel and Toledo, 1999), and ecosystem services (Dauber et al., 2005; Klein et al., 2003; Loreau et al., 2001; Vandermeer et al., 2010; Zhang et al., 2007). Enhancement of agricultural matrix quality results in additional food or nesting resources or better protection from predators, thereby favoring natural enemies (Gallego-Ropero et al., 2009; Landis et al., 2000; Vandermeer et al., 2010). Practices like providing artificial nesting sites, diverse plant species, or alternative food resources positively impact ecosystem services by increasing abundance of predators (Folgarait, 1998; Landis et al., 2000; Philpott and Foster, 2005; Teodoro et al., 2008). Thus, understanding which local and landscape factors drive ecosystem services is necessary in order to best promote specific pest control practices (Avelino et al., 2012; Tschardt et al., 2005).

1.3. Ants as potential predators in coffee farms

Ants are predators in coffee agroecosystems (De la Mora et al., 2008; Larsen and Philpott, 2010; Vandermeer et al., 2010), and ant diversity, abundance, and habitat complexity in coffee farms is positively associated with high pest removal (Armbrecht and Perfecto, 2003). Coffee intensification negatively affects pest control services provided by ants (Philpott and Armbrecht, 2006) and certain agricultural practices, like shade tree pruning or removal of coffee twigs, change structural characteristics of agroecosystems and may affect the abundance or predatory efficiency of ants (De la Mora et al., 2008; Larsen and Philpott, 2010; Philpott and Armbrecht, 2006; Philpott and Foster, 2005). Comparisons of local and landscape influences on ants find that local characteristics, such as insolation and soil conditions, more strongly affect ant communities than landscape factors (Dauber et al., 2005).

Ants, including those that nest and forage on the ground, coffee branches, or on trees, may positively affect coffee as biological control agents (Folgarait, 1998; Jiménez et al., 2008) and may specifically control coffee pests (Ibarra-Núñez et al., 2001; Philpott and Armbrecht, 2006). Ground- and coffee-foraging ants prey on the coffee berry borer (Armbrecht and Perfecto, 2003; Larsen and Philpott, 2010) and limit the coffee leaf miner (De la Mora et al., 2008). Coffee intensification and moving away from forest fragments negatively impacts control of coffee pests by ants (Armbrecht and Gallego, 2007; Armbrecht and Perfecto, 2003; Philpott and Armbrecht, 2006) likely because ant effects on pests depend on taxonomic and functional richness of ants in the community (Philpott and Armbrecht, 2006). Less is known, for coffee or other agroecosystems, about the relative influences of local agricultural management, components of the surrounding landscape, and the ant community, on predatory impacts of ants on pests.

1.4. Hypothesis and goals

The goal of this study is to examine relative impacts of local, landscape, and ant community factors on predation services provided by ants in coffee landscapes. We also examined the effects of seasonality on predation because population sizes and locations (e.g., on coffee plants or on the ground) of pests in the system can shift seasonally (Barrera, 2002). For example, the coffee berry borer (*Hypothenemus hampei* Ferrari), the most damaging insect pest of coffee, is more abundant on coffee plants during the rainy season, and on the ground during the dry season (Barrera, 2002). We examined how changes in agricultural management at the local (e.g., vegetation characteristics, agrochemical use) and landscape levels (e.g., distance from forest fragments, area of forest cover surrounding study sites) affect predatory activities of ants in coffee agroecosystems. We also examined whether changes in ant abundance or richness correlate with changes in predation services provided by ants. Specifically, we tested the following hypotheses: (1) ants remove prey items and prey removal differs in the wet and dry season, (2) ant prey removal differs with changes in vegetation complexity and agrochemical use, (3) ant prey removal differs with changes in ant abundance and species richness, and (4) ant prey removal differs with changes in local and landscape characteristics. We predicted that ant removal would be higher in the wet season, in sites with higher vegetation complexity and lower agrochemical use, and that several local and landscape factors would correlate with prey removal. Further, we expected prey removal to be higher near to forests and rustic coffee areas and with greater amounts of forest and rustic coffee surrounding the study sites.

2. Materials and methods

2.1. Study site

We conducted research in the Soconusco region of Chiapas, Mexico in an area dominated by coffee (~94% of the landscape) and forest fragments (~6% of the landscape) (Philpott et al., 2008b). Study sites were located 30–40 km NE of Tapachula between 800–1450 m above sea level, and receive 4500 mm of rain per year. We established forty 20 × 20 m sites; 10 in forest fragments and 30 in coffee sites. Our 30 coffee study sites could be classified as rustic (3 sites), traditional polyculture (4), commercial polyculture (7), shade monoculture (15), and 1 sun coffee (1) (according to Philpott et al., 2008a).

2.2. Local and landscape factors

In each site, we measured local and landscape characteristics. At the local scale, we measured 19 variables related to site location

(slope and terrain), vegetation (percent canopy cover, tree height, tree circumference, tree density, tree richness, number of coffee plants, number of hollow coffee twigs, number of rotten logs on the ground, length of rotten logs, circumference of rotten logs, degree of decay of rotten logs, leaf litter mass, and humus mass), and agrochemical use (frequency of use of fertilizers, pesticides, fungicides, and herbicides). With the 13 vegetation variables, we created a vegetation complexity index (VCI) to summarize vegetation changes across sites and to separate farm sites into 13 high- and 17 low-shade coffee habitats (Mas and Dietsch, 2005; De la Mora et al., 2013). The VCI was calculated by dividing values for each vegetation variable by the highest measured value to transform values from 0 to 1 (1 indicating more complex vegetation). For number of coffee plants, generally a negative correlate of vegetation complexity, we transformed values, then subtracted from 1. We summed transformed values of each variable for each plot, and divided by 7 to obtain the VCI value. We used data for the four agrochemical variables to create an agrochemical index (AI) calculated in the same way as the VCI. With a geographic information system of the study region and data analysis in ArcGIS, we calculated seven landscape-level factors: distance to the nearest forest patch and the percent of rustic coffee and forest within 50 m, 200 m, and 500 m buffer zones (see Philpott et al., 2008b). We used forest and rustic coffee for landscape variables for two reasons. First, ~100% of the study landscape is forest and coffee. Second, we were interested in examining the influence of forest and rustic coffee, the most forest-like coffee habitat (Moguel and Toledo, 1999), in provisioning of predation services. Local and landscape characteristics differed for forest, high-, and low-shade sites, and further details about sampling, values, and differences can be found in De la Mora et al. (2013) and in the Supplemental information (S1).

2.3. Predation trials

We examined ant predatory impacts during both the wet (June–August 2010) and dry seasons (February–April 2011). We assessed ant predatory impact by examining removal rates of two sentinel prey items, frozen (and presumed dead) West Indian fruit flies (*Anastrepha obliqua* Macquart) and coffee berry borers that were added to forest and coffee sites. In many studies with sentinel prey, prey items are restricted from moving by being glued (Armbrecht and Perfecto, 2003) or tethered (Jedlicka et al., 2011; Mathews et al., 2004) to observation locations. Other studies restrict prey movement by using frozen (and thus dead) prey items (e.g., Gardiner et al., 2014; Jones et al., 2001; O'Neal et al., 2005; Prasifka et al., 2006). We chose to use frozen prey, and acknowledge that this may have affected the community of ants removing the coffee berry borers or flies. Some species of scavenger ants may have been attracted to the sentinel prey, but may not feed on or hunt live prey items. We chose to use the coffee berry borers on the coffee plants and flies on the ground and trees only. Our choice of different prey in different strata may have influenced removal rates, but we chose to use borers on the coffee only as that is where this pest causes the economic damage to the coffee fruits, and we wanted to identify whether ants remove this pest in the field.

We quantified prey removal in three different strata – on the ground, on coffee plants (or on shrubs in forest sites), and on tree trunks. For ground trials we placed 20 fly adults on an index card (10 × 7 cm) and placed cards on the ground. For coffee trials, we placed 20 coffee berry borer adults (CBB) on an index card, and balanced cards between two coffee branches 1–1.50 m above ground. For tree trials, we put 20 fly adults on an index card and balanced cards 1.3 m above the ground on low branches of *Inga* spp. shade trees. For coffee and tree trials, we took care placing the cards, and bent cards slightly to ensure that missing prey were due

to predation and not because prey fell off. We placed two cards (between 8 a.m. and 2 p.m.) in each stratum in study site during both the dry and wet seasons in a different haphazardly selected location within the 20 × 20 m site. Thus we observed 40 prey total per site per season in each site. One observer watched each card continuously for 30 min, and recorded the number of prey items removed after 30 min.

We also recorded the number of ant individuals and the species (or morphospecies of ants) on the cards. At the end of the trial (after 30 min) we collected all ant individuals seen on cards, or that had recently left cards, for identification. Ants were stored in 70% ethanol and identified to species (or morphospecies) following Bolton (1994) and Longino (2009, 2011).

2.4. Data analyses

We compared prey removal rates in the three habitat types and during the two study seasons. We summed the number of prey items removed from the two cards in each site during each season and compared the number of prey items removed on the ground, on coffee plants (or shrubs), and on tree trunks with generalized linear mixed models (GLMM) with 'glmer' in the 'lme4' package in R (R Development Core Team, 2012). We used number of prey items (out of 40) as the dependent variable, and used the 'cbind' function, a binomial error distribution and logit link. We included habitat type and season, and the interaction between them as fixed factors and included the number of ant species, individuals, or both counted on cards as random factors.

We next examined relationships between prey removal on the ground, coffee or shrubs, and shade trees and vegetation complexity (VCI), agrochemical use (AI), ant richness, and ant abundance. We took the mean number of prey items removed across the two seasons and used site as a replicate. We examined ant abundance and richness in two ways. First, we examined richness and abundance observed on index cards where we placed prey items. For abundance, we calculated the mean number of individuals recorded per card during each min over the 30 min observation, thus the mean number of individuals per card was in some cases less than one individual. For richness, we counted the number of different ant morphospecies visiting cards in 30 min. Second, we examined total ant richness and abundance as determined with extensive ant surveys in each study site (De la Mora et al., 2013). We used data from mini-Winkler traps and rotten log samples for ground ant abundance and richness, data from coffee twig surveys for coffee/shrub ant abundance and richness, and data from baits placed on tree trunks for tree ant abundance and richness (De la Mora et al., 2013). Only ants from each stratum (ground, coffee twigs, and tree trunks) were used as correlates of removal on the ground, coffee plants, and trees respectively. We examined relationships between prey removal and explanatory variables with generalized linear models (GLMs) in R with the 'cbind' function, a binomial error distribution and logit link. Based on the GLM results, we used ANOVA with chi-square statistics to estimate the *P*-values, and used a Bonferroni correction to account for multiple tests (6) per dependent variable (adjusted $\alpha = 0.008$).

To examine which factors influenced prey removal rates we created conditional inference trees with the 'party' package in R (Hothorn et al., 2006; R Development Core Team, 2012). We ran three sets of conditional inference trees, one for each prey removal strata (ground, coffee or shrubs, and tree trunks). For each stratum, we used three separate models. In the first model, we included 19 local- and 7 landscape-scale habitat variables as predictors of prey removal. In the second model, we included 19 local- and 7 landscape-scale variables and abundance and richness of ants observed on cards as predictors of prey removal. In the third model,

we included 19 local- and 7 landscape-scale variables and total abundance and richness (measured in extensive ant surveys) as predictors of prey removal. For all tests, we used the minimum criterion of 0.95 ($P=0.05$), and used the site as a replicate.

We examined for spatial autocorrelation (Dormann et al., 2007) in residuals of the conditional inference trees and GLMs with (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; Bjornstad, 2009; R Development Core Team, 2012). For the correlograms, we computed 100 permutations using the *resamp* argument in the *correlog* function to examine the distance at which variables were autocorrelated. For the calculation of Moran's I, we used nearest neighbor distances as the metric, and used the permutation test option. One of 27 of the statistical tests examined displayed significant spatial autocorrelation (Table S1), thus spatial autocorrelation is likely not pervasive.

3. Results

3.1. Prey removal rates in different habitats and during different seasons

Prey removal on the ground, on coffee or forest shrubs, or on trees did not differ with habitat type (forest, high-shade coffee, and low-shade coffee). Ants removed 3.15 ± 1.20 (SE) prey items from the ground in forests, 5.0 ± 1.14 in high-shade coffee, and 3.62 ± 0.88 in low-shade coffee. Ants removed 4.0 ± 0.71 prey items in the dry season and 3.9 ± 0.99 prey items in the wet

season. On coffee and shrubs, ants removed 0.20 ± 0.12 prey items in forests, 2.35 ± 0.74 in high-shade coffee, 2.62 ± 1.08 in low-shade coffee, 2.10 ± 0.79 in the dry season, and 1.75 ± 0.71 in the wet season. On shade tree trunks, ants removed 1.45 ± 0.99 prey in forests, 2.88 ± 1.12 in high-shade coffee, 3.38 ± 0.81 in low-shade coffee, 3.73 ± 0.89 in the dry season, and 1.75 ± 0.64 in the wet season. According to the likelihood ratio test, for each of the three strata, the best model including habitat type and season as fixed factors, and ant individuals (ground, coffee/shrub) or ant individuals and species (tree) as random factors were not significantly different than the null (intercept only) models for each strata (ground, $P=0.194$; coffee/shrub, $P=0.705$; tree, $P=0.178$). Thus habitat and season did not provide increased predictive power of the variation in prey removal by ants.

3.2. Vegetation complexity, agrochemical use, and prey removal

Vegetation complexity (Fig. 1), but not agrochemical use correlated with prey removal on coffee/shrubs and on trees. According to the GLM, there was no correlation between the vegetation complexity index (VCI) and prey removal on the ground ($z = -1328$, $X^2 = 1.785$, $df = 1$, 38 , $P = 0.1815$), but VCI was negatively correlated with prey removal on coffee ($z = -3.899$, $X^2 = 16.683$, $df = 1$, 38 , $P < 0.001$), and trees ($z = -2.812$, $X^2 = 8.273$, $df = 1$, 38 , $P = 0.004$). There was no correlation between the agrochemical index (AI) and prey removal on the ground ($z = -0.395$, $X^2 = 0.157$, $df = 1$, 38 , $P = 0.692$), on coffee ($z = -0.134$, $X^2 = 0.018$, $df = 1$, 38 , $P = 0.893$), or on trees ($z = 0.09$, $X^2 = 0.008$, $df = 1$, 38 , $P = 0.929$).

Fig. 1. Relationships between vegetation complexity, ant abundance on observation cards, ant richness on observation cards, ant abundance at a site, and ant richness at a site and prey removal from the ground (top row), from coffee plants (middle row) and from shade tree trunks (top row) in forests and coffee agroecosystems in Chiapas, Mexico. Panels show results for 40 sites including low-high shade and forest. Trend lines and regressions are shown for significant relationships as determined by GLM: * where $P < 0.01$, and ** where $P < 0.001$.

3.3. Ant abundance and richness and prey removal

Local abundance and richness of ants (observed on cards) and total abundance correlated significantly with prey removal on all strata (Fig. 1). We observed 50 different morphospecies of ants from 21 genera: *Pheidole* was the most species rich genus with 19 morphospecies observed. Overall, ants removed 239 prey items, and 11 morphospecies removed 62% of prey items removed (Table 1). Prey removal was positively correlated with number of ant individuals on cards on the ground ($z = 7.304$, $X^2 = 52.361$, $df = 1$, 38 , $P < 0.001$), on coffee ($z = 9.892$, $X^2 = 85.439$, $df = 1$, 38 , $P < 0.001$), and on trees ($z = 6.274$, $X^2 = 34.598$, $df = 1$, 38 , $P < 0.001$). Prey removal was also positively correlated with the number of ant species that visited index cards on which prey items were placed on the ground ($z = 6.946$, $X^2 = 54.376$, $df = 1$, 38 , $P < 0.001$), on coffee and shrubs ($z = 5.335$, $X^2 = 27.933$, $df = 1$, 38 , $P < 0.001$), and on trees ($z = 6.668$, $X^2 = 43.279$, $df = 1$, 38 , $P < 0.001$).

Total ant richness and abundance correlated with prey removal on trees, but not on the ground or on coffee or shrubs. Prey removal on trees was significantly correlated with total ant richness ($z = 4.693$, $X^2 = 20.705$, $df = 1$, 38 , $P < 0.001$) and total ant abundance ($z = 4.68$, $X^2 = 20.429$, $df = 1$, 38 , $P < 0.001$). Prey removal on the ground did not correlate with total ant species richness ($z = -0.753$, $X^2 = 0.566$, $df = 1$, 38 , $P = 0.452$) or abundance ($z = 0.810$, $X^2 = 0.660$, $df = 1$, 38 , $P = 0.417$) as determined with extensive surveys. Likewise, prey removal from coffee plants and shrubs did not vary with total richness ($z = 1.79$, $X^2 = 3.21$, $df = 1$, 38 , $P = 0.07$) or abundance ($z = 0.896$, $X^2 = 0.782$, $df = 1$, 38 , $P = 0.376$).

3.4. Local and landscape factors and prey removal rates

Conditional inference trees showed that ant abundance and richness (on cards and total richness measured in extensive surveys) were the most important factors driving prey removal when included in the regression tree model. In the models without ant variables, local factors were more important predictors of prey removal than landscape factors. For the model including only local and landscape factors, ground prey removal positively correlated with one local factor (number of hollow coffee twigs) (Fig. 2a), coffee/shrub prey removal was influenced by one local factor (coffee plant density) and one regional factor (rustic coffee area within 200 m) (Fig. 2b), and tree prey removal was not influenced by any local or landscape factor. For the model that included local and landscape habitat factors, plus richness and abundance of ants observed on cards, ground prey removal positively correlated with ant abundance (Fig. 2c), and coffee/shrub prey removal (Fig. 2d) and tree prey removal (Fig. 2e) were positively correlated with ant abundance and ant richness. For the model that included local and landscape factors and total ant richness and abundance, prey removal on the ground and in coffee/shrubs did not differ from the

first model; however, tree prey removal increased with increased ant richness (Fig. 2f).

4. Discussion

4.1. Season, habitat, and vegetation and agrochemical indices

Prey removal on trees was higher in coffee farms than in forests, and prey removal on coffee/shrubs and trees declined with increases in vegetation complexity, but prey removal on the ground did not differ with habitat or vegetation complexity. This was unexpected, as ant predation often declines with decreasing vegetation complexity. For example, in Colombia, reductions of canopy cover or tree diversity in coffee systems results in lower prey removal rates by ants (e.g., Armbrrecht and Perfecto, 2003; Armbrrecht and Gallego, 2007). In Mexico, CBB removal rates from coffee plants are higher in farms with higher tree density and diversity (Larsen and Philpott, 2010). Higher removal rates in the lower canopy (e.g., tree trunks) and on shrubs in sites with higher canopy complexity may be due to differences in available canopy resources. For example, canopy trees may have more abundant hemipteran and extra-floral nectar resources compared with understory trees and as such maintain high densities of arboreal ants in the canopy (e.g., Blüthgen and Stork, 2007; Rico-Gray and Oliveira, 2007). It may be possible that in high canopy complexity sites, canopy resources may be abundant enough to supply resources needed by colonies such that arboreal ants need not forage in the lower canopy or shrubs. In contrast, low canopy complexity sites, with presumably fewer hemipteran and prey resources, ants must forage in all strata in order to find sufficient resources. This may explain higher removal on tree trunks or shrubs in less complex habitats. In addition, because two of the factors included in the calculation of the VCI relate to leaf litter and four factors relate to rotting logs on the ground, some of the observed changes (or lack thereof) in prey removal with changes in the VCI may relate to shifts leaf litter and soil resources, or the biodiversity supported by these resources. Interestingly, others have not isolated whether differences in removal rates are due to structural changes in habitat complexity or to differences in the predatory ant community. A lack of differences between habitat types, but significant differences with the vegetation complexity index (VCI) may be because of the more specific description of each site provided by the VCI as compared with the categorical variable of habitat type.

Surprisingly, we did not find a relationship between prey removal and agrochemical use. Agrochemical applications negatively affect ant richness and abundance (Andersen et al., 2002; McCoy et al., 2001) and negatively affect natural enemies thereby reducing predation rates (Leslie, 1977; McCoy et al., 2001). In our study area, agrochemicals including endosulfan, chlorpyrifos, and copper sulfate are sprayed to control insect pests (e.g., CBB) and fungal diseases (García Estrada et al., 2006; Jaramillo et al., 2006).

Table 1

Top eleven ant morphospecies that removed sentinel prey from index cards in three habitats (forest, high-shade coffee, and low-shade coffee) in Soconusco, Chiapas.

Ant species ^a	Removal from tree trunks ^b	Removal from coffee or shrubs	Removal from the ground
<i>Pheidole protensa</i>	1	0	34
<i>Pheidole synanthropica</i>	7	2	17
<i>Pheidole</i> sp. 16	0	5	11
<i>Pheidole</i> sp. 11	4	4	6
<i>Pheidole</i> cf. <i>pubiventris</i>	6	2	3
<i>Gnamptogenys striatula</i>	1	1	7
<i>Pheidole</i> sp. 10	0	0	9
<i>Nylanderia</i> sp. 1	2	3	2
<i>Pheidole</i> sp. 1	0	0	7
<i>Solenopsis globularia</i>	0	0	6
<i>Wasmannia auropunctata</i>	1	1	4

^a Ant species are organized from the morphospecies that removed the most prey items across all sites to those that removed fewer prey items.

^b Numbers show the total numbers of prey items removed by that ant species in that stratum across all plots and all habitat types.

Fig. 2. Conditional inference trees examining relationships between 19 local and 7 regional factors and ant richness and abundance and prey removal. Graphs show the influences of local and landscape predictors only on prey removal on (a) the ground and (b) coffee plants, the influences of local and landscape predictors, plus local ant richness and abundance on prey removal on the (c) ground, (d) coffee plants, and (e) shade trees, and influences of local and landscape predictors, plus total ant richness and abundance on prey removal on the (a) ground, (b) coffee plants, and (f) shade trees. 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 (gray box), the median values (solid black line), and $1.5 \times$ the inner quartiles (error bars) of ant abundance associated with each string of predictor variables. Sample sizes at each terminal node show the number of sites in that box plot. The number of ant individuals per card is the average number of ants seen each minute over the 30 min observations.

All of these chemicals can affect predatory ants (Andersen et al., 2002; McCoy et al., 2001). In our study, *Pheidole* spp. removed a high (60%) fraction of prey removed, yet chemicals sprayed (e.g., glyphosate) can negatively impact *Pheidole* abundance (Leslie, 1977). In fact, in our study, the number of *Pheidole* colonies in study sites declined with increased agrochemical use ($R^2 = 0.12$, $F_{1,38} = 4.925$, $P = 0.033$). In contrast, other agrochemicals, such as fertilizer, may indirectly increase ant predatory activities. For example, with synthetic fertilizers, populations of hemipteran pests like aphids and scale insects may increase, resulting in increased activity of hemipteran-tending ants, many of which are also predatory (Strauss, 1987). Certain agrochemicals may vary in their effects on ants and predatory activity (Andersen et al., 2002), but because we combined effects of all agrochemicals on into one index, the individual, slightly nuanced effects of different chemicals used may have been thus masked.

Ant predatory activities often differ in tropical wet and dry seasons, but we did not observe seasonal changes in prey removal. In tropical rainforests, protein requirements (and hence prey removal) by arboreal and ground-foraging ants vary seasonally (Davidson et al., 2003; Hahn and Wheeler, 2002). In forests, composition of ant species attracted to baits varies seasonally with terrestrial ants moving onto arboreal baits more often in the wet season (Hahn and Wheeler, 2002). In studies in South America, CBB removal rate is higher in habitats with greater shade cover in the rainy season (Armbrecht and Gallego, 2007), perhaps because CBB densities are higher in the rainy season (May–July) (Teodoro et al., 2009). Environmental factors, such as increased soil temperature and high and low soil moisture (Baccaro et al., 2010; Porter and Tschinkel, 1987; Teodoro et al., 2010; Ruano et al., 2000), desiccation risk (Baccaro et al., 2010), and heavy rainfall (Porter and Tschinkel, 1987) may all lower foraging activity of particular ant species. Despite all this evidence that ant foraging and predation may differ with season, we did not observe seasonal differences in removal rates. In our study, differences in the composition of ants on baits during the wet and dry season, as well as different nutritional requirements or foraging rates of different species of ants during different seasons may make interpreting these community level removal effects more difficult.

4.2. Local and landscape factors and prey removal rates

When ant variables were not included in regression tree models, two local vegetation factors, and one landscape factor were positively associated with prey removal rates. Changes in structural characteristics of agroecosystems, including reductions in habitat or landscape complexity, may hinder ecological services like predation, parasitism, and pollination (Chaplin-Kramer et al., 2011; Fahrig, 2003; Tschirntke et al., 2005). Generally, changes to the physical structure and vegetation complexity of farms impact richness and abundance of ants because of alterations to microclimatic conditions, food availability, and availability of nesting sites (Moguel and Toledo, 1999; Andersen and Majer, 2004; Perfecto and Vandermeer, 1996; Philpott and Armbrecht, 2006; Teodoro et al., 2010). We demonstrated that specific vegetation characteristics of coffee habitats (numbers of hollow coffee twigs and number of coffee plants in a site) positively correlate with prey removal from the ground and from coffee plants; no local habitat factors influenced prey removal on trees. Increased numbers of hollow coffee twigs leads to increases in abundance of arboreal twig-nesting ants (Philpott and Foster, 2005), and perhaps where coffee twigs are abundant, there is a high density of hollow twigs on the ground. In other coffee systems, increases in the density and diversity of hollow twigs on the ground increase the abundance and richness of ground-foraging predatory ants (Armbrecht et al., 2004), and

thus may increase predation rates. In addition, abundance of trees and coffee plants may influence solar radiation or soil temperatures (Lin, 2007), and both of those factors may influence ant activity and prey removal rates (Kaspari and Weiser, 2000). At the landscape scale, rustic coffee within 200 m was negatively correlated with prey removal on coffee and shrubs. In our sites, rustic coffee sites were closer to forest fragments, and may have higher abundance of prey and other resources for ants (e.g., nectar, canopy hemipterans) that may pull arboreal-foraging ants away from the introduced prey resources. In other studies, however, proximity to vegetatively complex areas enhances predation (Armbrecht and Perfecto, 2003; Dauber et al., 2003).

4.3. Ant abundance, richness, and prey removal

Our data support the hypothesis that richness and abundance of ants observed in predation trials positively correlated with prey removal rates in a coffee agroecosystem, but total richness and abundance of ants had a more limited influence on prey removal. We found that local abundance and richness of ants was positively and strongly correlated with proportion of prey removed from the ground, coffee, and trees, and that the changes in the ant community were more important than other local and landscape factors. Total ant richness in a site was correlated with prey removal on trees, but not on the ground or coffee plants and total colony abundance did not influence prey removal in any strata. Our experiments focused on observing prey removal, and thus ants observed on cards act as predators of the specific prey items that we studied. Within the overall community in a site, many species may not be predatory, may forage in different strata, may forage at other times of day or year that we did not test, and still others may specialize on other prey items. Thus in effect, we have isolated that fraction of the ant community preying on fly and CBB prey items in coffee habitats. This distinction between actually observing predators, and attempting to correlate overall arthropod populations on plants with or without ants may be one reason why some other studies did not observe strong correlations between ant richness and arthropod reduction (e.g. Larsen and Philpott, 2010). Of course, increased removal of prey by ants due to increases in abundance or richness could actually be mediated by other changes, such as differences in vegetation, temperature, or humidity. The fact that ant community variables were the most important predictors of prey removal (and more important than the local and landscape factors) in the inference trees is a strong indication that these variables play an important role in determining the degree to which prey are removed. An important caveat to our study is that we used frozen (and thus dead) prey items. Thus, some of the ant species that removed the borers and flies may be more accurately described as scavengers. Nonetheless, many species in the same genera that we observed removing prey items (e.g., *Pheidole*, *Solenopsis*, *Gnamptogenys*, *Wasmannia*) remove live berry borers from coffee fruits and other types of exclosures (e.g., Armbrecht and Perfecto, 2003; Armbrecht and Gallego, 2007).

There are several mechanisms that may link increased ant richness to increased prey removal. First, increased richness may result in increased presence of a single important predator (i.e., the sampling effect (Huston, 1997)). We cannot rule out that explanation, but we did observe several genera of ants removing prey items in each strata (e.g., *Pseudomyrmex*, *Camponotus*, *Gnamptogenys*, *Pheidole*) hinting to the idea that the ant assemblage, rather than a single important species, is suppressing pests in the study sites. Second, complementarity among species may lead to increased predation (Ibarra-Núñez et al., 2001; Loreau and Hector, 2001; Loreau et al., 2001). Complementarity is based on the idea that different species differ in resource requirements, foraging behavior, or morphological features resulting in greater overall use

of available resources (see Loreau and Hector, 2001; Philpott et al., 2009). The different ant species and genera that we observed preying on flies and the CBB vastly differ in terms of eye and mandible morphology (Jiménez et al., 2008), as well as foraging behavior (Traniello, 1989). Such differences may lead to complementarity and subsequent increases in predation (Armbrecht and Perfecto, 2003; Philpott and Armbrecht, 2006). In coffee agroecosystems, other predators are complementary both in timing of predation events (e.g., birds and bats, ants and spiders) (Williams-Guillén et al., 2008; Ibarra-Núñez et al., 2001) and in terms of foraging strategy, strata, and morphology (e.g., birds, Philpott et al., 2009) leading to increases in removal of arthropods from coffee plants (Van Bael et al., 2008).

In general, agroecosystem intensification can lead to decreases in functional diversity organisms responsible for provisioning of ecosystem services (Tscharntke et al., 2005). For predation services in particular, we have identified that richness and abundance of ants, more so than differences in habitat type, vegetation complexity, or landscape characteristics play an extremely important role in determining overall predation rates. Because it is likely difficult to manipulate ant richness directly, steps could be taken to examine which vegetation factors relate to increases in richness and abundance of predatory ants, and then to change management to increase predation services. Other studies have documented specific factors that correlate with increases in abundance and species richness of ants in coffee agroecosystems (e.g., Philpott et al., 2008a; De la Mora et al., 2013), but have not explicitly focused on ants involved in predatory functions.

5. Conclusions

This study is the first to simultaneously examine the impacts of local, landscape and ant community drivers of prey removal by ants in a coffee landscape. One major finding of our study is that protection of biodiversity within agroecosystems supports ecosystem services. We document that increases in species richness and abundance of ants participating in pest removal services was highly positively correlated with prey removal rates, and likely increases the level of pest control services provided for this important agroforest crop. A second major finding of the study is that of all those local and landscape factors included in our predictive models of predation few correlate with prey removal, and of those that do, more are local than landscape factors. The number of hollow twigs (a local factor) was the only factor that correlated with removal on the ground, and the number of coffee plants (a local factor) and rustic coffee within 200 m (a landscape factor) were the only to correlate with removal from coffee plants and shrubs. No local or landscape factors correlated with removal from trees. Interestingly, one interesting implication of this study for farmers may be that increasing coffee density, that likely increases yields for farmers, is also positively associated with increased removal of coffee pests. A third major finding is that ant richness and abundance were overwhelmingly the most important correlates of prey removal. Thus, it appears that changes in the vegetation or habitat management predominantly affect prey removal rates via indirect effects on the ant community. We recommend that farmers take management actions to alter coffee farms in a way that increases ant richness and abundance in order to promote predation services.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2014.11.006>.

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