

Local and landscape drivers of biodiversity of four groups of ants in coffee landscapes

A. De la Mora, C. J. Murnen & S. M. Philpott

Biodiversity and Conservation

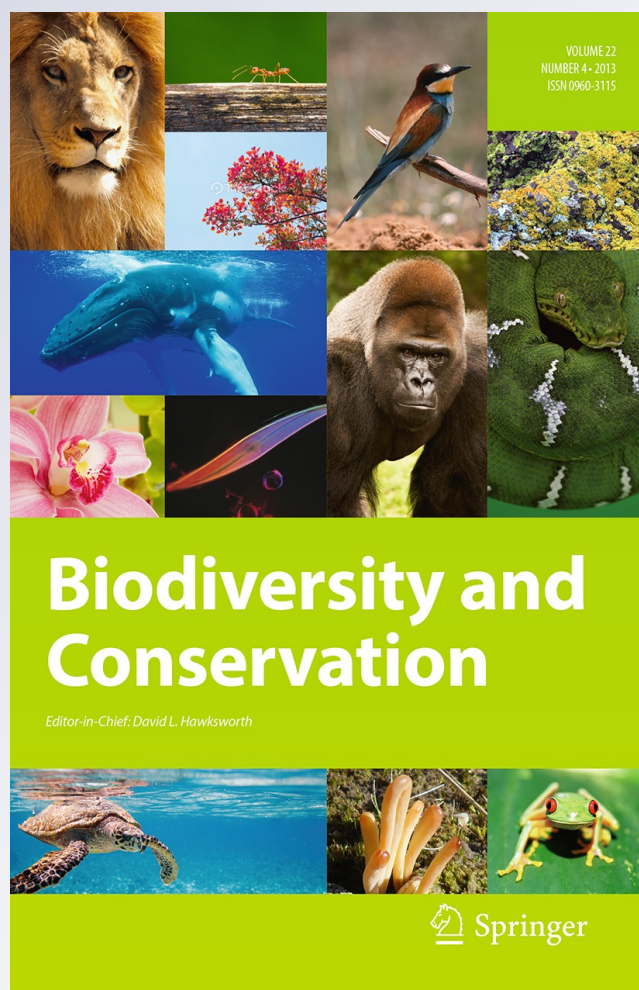
ISSN 0960-3115

Volume 22

Number 4

Biodivers Conserv (2013) 22:871-888

DOI 10.1007/s10531-013-0454-z



Your article is protected by copyright and all rights are held exclusively by Springer Science +Business Media Dordrecht. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.

Local and landscape drivers of biodiversity of four groups of ants in coffee landscapes

A. De la Mora · C. J. Murnen · S. M. Philpott

Received: 14 June 2012 / Accepted: 15 February 2013 / Published online: 12 March 2013
© Springer Science+Business Media Dordrecht 2013

Abstract Agriculture of varying management intensity dominates fragmented tropical areas and differentially impacts organisms across and within taxa. We examined impacts of local and landscape characteristics on four groups of ants in an agricultural landscape in Chiapas, Mexico comprised of forest fragments and coffee agroecosystems varying in habitat quality. We sampled ground ants found in leaf litter and rotten logs and arboreal ants found in hollow coffee twigs and on tree trunks. Then using vegetation and agrochemical indices and conditional inference trees, we examined the relative importance of local (e.g. vegetation, elevation, agrochemical) and landscape variables (e.g. distance to and amount of nearby forest and rustic coffee) for predicting richness and abundance of ants. Leaf litter ant abundance increased with vegetation complexity; richness and abundance of ants from rotten logs, twig-nests, and tree trunks were not affected by vegetation complexity. Agrochemical use did not affect species richness or abundance of any ant group. Several local factors (including humus mass, degree of decay of logs, number of hollow twigs, tree circumference, and absence of fertilizers) were significant positive predictors of abundance and richness of some ant groups. Two landscape factors (forest within 200 m, and distance from forest) predicted richness and abundance of twig-nesting and leaf litter ants. Thus, different ant groups were influenced by different characteristics of agricultural landscapes, but all responded primarily to local characteristics. Given that

Electronic supplementary material The online version of this article (doi:[10.1007/s10531-013-0454-z](https://doi.org/10.1007/s10531-013-0454-z)) contains supplementary material, which is available to authorized users.

A. De la Mora (✉)

Departamento de Entomología Tropical, ECOSUR, Carretera Antigua Aeropuerto Km 2.5,
Tapachula, Chiapas, Mexico
e-mail: aldodelamora@gmail.com

C. J. Murnen · S. M. Philpott

Department of Environmental Sciences, University of Toledo, 2801W. Bancroft Street,
MS 604, Toledo, OH 43606, USA

S. M. Philpott

Department of Environmental Studies, University of California, Santa Cruz, 1156 High Street,
Santa Cruz, CA 95064, USA

ants provide ecosystem services (e.g. pest control) in coffee farms, understanding ant responses to local and landscape characteristics will likely inform farm management decisions.

Keywords Agroecosystem · Biodiversity · Fragmentation · Matrix quality · Landscape ecology

Introduction

Humans have transformed tropical landscapes into landscapes characterized by an array of fragmented forests and anthropogenic land uses—including agriculture (Clergue et al. 2005). Both agricultural management and arrangement of different habitat patches in the landscape can affect biodiversity, making agricultural landscapes unique areas in which to study impacts of local and landscape-level factors on patterns of species abundance and richness (Tylianakis et al. 2005). In particular, agroforestry management ranges from intense farming where little to no tree canopy exists and high amounts of agrochemicals are used to traditional agroforests with some natural forest canopy and little use of agrochemicals (Tschardt et al. 2005).

Agroecosystems that mimic nearby natural areas support higher levels of biodiversity, and are referred to as high-quality matrices (Jules and Shahani 2003). The agricultural matrix is defined as homogenous, ecologically unimportant land that lacks resources necessary to support a local population (Vandermeer and Carvajal 2001), but is often underestimated for its ability to support biodiversity (Clergue et al. 2005; Tylianakis et al. 2005). A high-quality matrix facilitates inter-fragment dispersal (e.g. Castellon and Sieving 2006; Steffan-Dewenter et al. 2002; Vandermeer and Carvajal 2001), and provides habitat for pollinators and predators (Bianchi et al. 2006; Jha and Vandermeer 2010; Tylianakis et al. 2005). Arrangement of habitat patches, and distance from forest also affects biodiversity (Ricketts et al. 2001). Thus, both local site characteristics (land use type) and landscape factors (i.e. arrangement of habitats, degree of fragmentation) affect biodiversity in agricultural landscapes (Dauber et al. 2003; Duffy 2009; Tylianakis et al. 2005). An increasing number of studies have quantified landscape influences on biodiversity in agroecosystems (e.g. Concepción et al. 2008; Gibb et al. 2006; Økland et al. 1996), especially in the tropics (Batáry et al. 2010) but relatively few have compared both local and landscape influences (Gabriel et al. 2010; Schmidt et al. 2008).

One agricultural management system highlighted for conservation value is coffee. Biodiversity in coffee landscapes responds to agricultural management and farm location within the landscape (e.g. Armbrrecht et al. 2005; Moorhead et al. 2010; Perfecto and Vandermeer 2002). Rustic coffee agroecosystems, where coffee grows under a forest canopy (Moguel and Toledo 1999), are habitats that maintain biodiversity (Philpott et al. 2008a). However, intensive coffee production calls for canopy reduction or removal to increase productivity (Perfecto and Vandermeer 1996; Perfecto et al. 1996; Teodoro et al. 2010), and is accompanied by increased use of agrochemicals (García Estrada et al. 2006), which can exacerbate negative impacts on biodiversity (García Estrada et al. 2006; Philpott et al. 2008a). In addition, functional richness may decline with intensification thereby affecting ecosystem services in agricultural landscapes (Armbrrecht and Perfecto 2003; Jha and Vandermeer 2010; Perfecto and Vandermeer 2002; Philpott et al. 2008a).

Ants comprise a large fraction of the animal biomass in the tropics (Hölldobler and Wilson 1990). Ants are sensitive to habitat changes (Andersen et al. 2002;

Peck et al. 1998), and are often used to assess ecosystem responses to land management (Andersen and Majer 2004; Hoffmann 2010). Local factors that correlate with ant richness in tropical landscapes include leaf litter biomass and depth, tree richness, tree abundance, and overall intensity of crop production (Armbrecht and Perfecto 2003; Bisseleua et al. 2009; McGlynn et al. 2009; Perfecto and Vandermeer 2002; Philpott et al. 2008a). Ant richness also responds to landscape characteristics such as distance from forest and forest fragment size (Dauber et al. 2003; Perfecto and Vandermeer 2002). However, little research examines relative impacts of local and landscape factors for ant species richness and abundance in agricultural landscapes.

We examined abundance and richness for four ant groups in a coffee landscape. Our goal was to examine effects of local (e.g. vegetation, agrochemical use) and landscape characteristics (distance from forest, land cover types in the surrounding landscape) on ant communities. We studied two groups of ground ants: leaf litter ants and ants nesting in rotten logs; and two groups of arboreal ants: twig-nesting ants in coffee twigs, and ants foraging on tree trunks (hereafter arboreal ants) in a landscape containing coffee farms differing in management intensity and forest fragments. Specifically, we asked: (1) Does abundance and richness of different ant groups vary in forests and coffee farms differing in management intensity? (2) Which local and landscape level characteristics correlate with abundance and richness of different ant groups? (3) Do ants primarily respond to changes in local or landscape level characteristics, and (4) Do different groups of ants respond to local and landscape level characteristics in similar ways?

Materials and methods

Study site

We conducted research in Soconusco, Chiapas, Mexico in a 52 km² area dominated by coffee (~94 % of the landscape) and forest fragments (~6 % of the landscape) (Philpott et al. 2008b), (Fig. 1). Study sites were located near Tapachula within the coordinates 15.202N, 92.383W (NW corner) and 15.144N, 92.297W (SE corner) between 800 and 1450 m above sea level. Rainfall averages 4500 mm per year with a dry season between December and April. We established 40 20 × 20 m sites; ten in forest fragments and 30 in coffee farms. Sites were 25–1110 m from the forest edge. Shade management in coffee sites was distributed along the full range from rustic to sun management (Moguel and Toledo 1999), and we assigned coffee sites to high- and low-shade treatments based on vegetation (see below). Further, 22 of 30 coffee sites experienced at least one agrochemical application during the study year.

Local site characteristics

We measured local characteristics including vegetation, elevation, slope, leaf litter and humus mass, and agrochemical use. The vegetation data measured were: (a) percent canopy cover, (b) tree height, (c) tree circumference 1.37 m above ground, (d) tree density, (e) number of coffee plants, (f) tree species richness, (g) number of hollow coffee twigs, (h) number of rotten logs on the ground, (i), circumference of rotten logs, and (j) degree of decay of rotten logs. We measured canopy cover with a GRS densitometer at the center and four corners of each site. We estimated tree height for trees <15 m and measured trees ≥15 m with a rangefinder (Bushnell, Overland Park, Kansas). We assessed log decay with

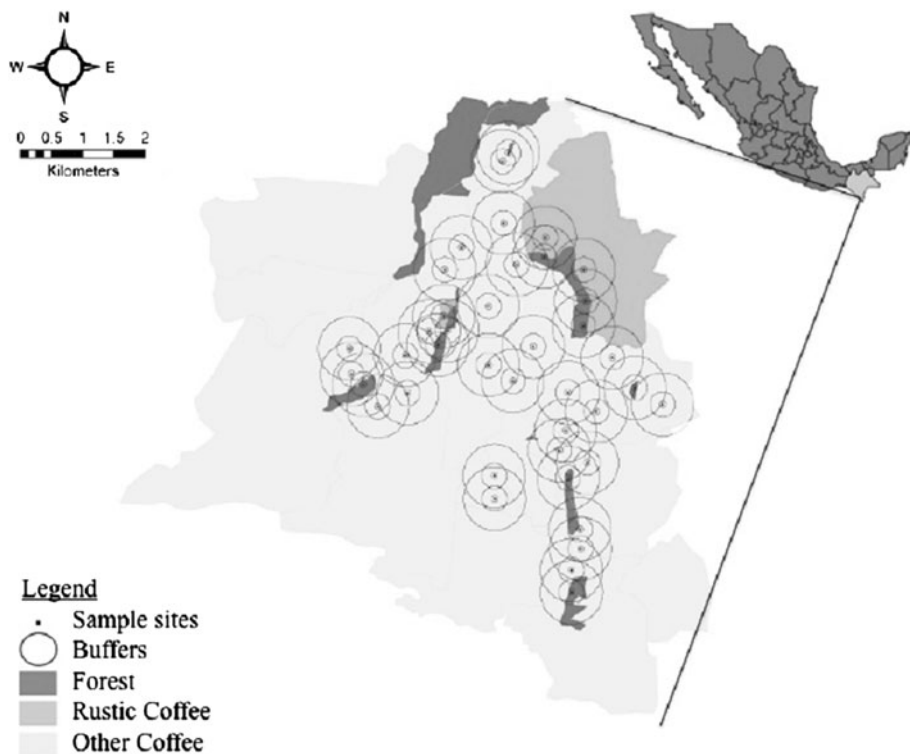


Fig. 1 Map of the study landscape in the Soconusco region of Chiapas, Mexico. Circles around each site represent 50, 200 and 500 m buffers

classes (modified from Torres 1994): (1) hard bark intact, (2) bark present, sapwood partly soft, bark easy to remove with hands, (3) no or partly removed bark, soft sapwood, (4) no bark and sapwood easily breakable with an axe, and (5) no bark, wood resembles humus. We recorded elevation with a Garmin GPS 60 and assessed slope with a clinometer (Suunto PM5/360PC). We weighed sifted leaf litter and humus collected in leaf litter ant plots (see below) using a hand held spring balance. We interviewed farm personnel to quantify pesticide, herbicide, fertilizer, and fungicide use in each site (Table S1). We did not collect data on the frequency with which certain brands of chemicals were used, but in the study area, commonly used agrochemical products include Thiodan (endosulfan, an organophosphate insecticide used to control *Hypothenemus hampei*), Round-up (glyphosate, a broad-spectrum herbicide used to control weeds), copper sulphate fungicides, and urea.

To summarize vegetation and agrochemical data, we created two indices: (a) a vegetation complexity index (VCI) (Philpott et al. 2008a) and (b) an agrochemical index (AI). To calculate the VCI we divided values for each variable by the highest observed measurement, transforming values from 0 to 1 (1 indicating more complex vegetation). For coffee density, which negatively correlates with vegetation complexity, we transformed values from 0 to 1, then subtracted from 1. We summed transformed values for each variable for each site, and divided by the total number of variables measured in that site to yield the VCI value. We used VCI values to classify coffee sites into high- (13 sites with

VCI between 0.37 and 0.609) and low-shade coffee (17 sites with VCI between 0.029 and 0.35). For AI, we counted the number of applications of each type of agrochemical each year, and divided by the highest observed number of applications across sites. We then summed values for each agrochemical, and divided by the number of agrochemicals used to yield the index values from 0 to 1 where 1 indicates high use of agrochemicals.

Landscape factors

We characterized the landscape surrounding each site with a geographic information system (GIS) modified from Philpott et al. (2008b). Philpott et al. (2008b) used a multi-spectral, panchromatic IKONOS[®] image and digital elevation model taken on December 10th, 2005 to create a land use map for the study area. We updated the GIS in November–December 2009 by: (1) taking GPS points around all forest fragments, and (2) validating coffee management type for each farm. Two coffee farms were classified as rustic coffee; all other coffee farms were classified as other coffee. In ArcGIS, we calculated for each site (a) distance to the nearest forest edge, (b) the area of forest within 50, 200 and 500 m buffers surrounding the study sites, and (c) the area of rustic coffee within 50, 200 and 500 m buffers. We chose those buffer sizes following others who have studied landscape effects on ants (e.g. Dauber et al. 2005).

Ant sampling protocol

We sampled four groups of ants during dry (February–March) and wet seasons (June–July) of 2010. We sampled leaf litter ants following standard protocol for mini-Winkler traps (Agosti and Alonso 2000). We collected ants from two randomly located 1 × 1 m plots per site during each season for a total of 160 samples. We hung mini-Winkler traps for 72 h and trapped ants in cups with 70 % ethanol. We sampled ants nesting in rotten logs with destructive sampling. We examined fallen logs and branches for 3 h per site per season by opening all logs with machetes and axes while searching for ants. We sampled arboreal twig-nesting ants in two 10 × 10 m sub-plots in each site; one sub-plot per season. We hereafter refer to all arboreal twig-nesting ants simply as twig-nesting ants. We did not sample twig-nesting ants on the ground. We broke dry twigs off each coffee plant and recorded the number of dry twigs, hollow twigs, and twigs occupied by ants. All coffee plant twigs were lower than 2.5 m off the ground, and were easily accessible. Finally, we sampled arboreal ants on tree trunks with protein (West Indian fruit fly, *Anastrepha obliqua*) and carbohydrate (sugar cane) baits (Bestelmeyer et al. 2000). We glued 20 dead flies or placed 5 g of sugar cane on index cards (10 × 7 cm), and attached cards to *Inga* spp. shade trees at 1.3 m above ground with tacks. We observed baits on four *Inga* trees per site per season, two with flies and two with sugar cane. We waited for 30 min, and recorded and collected all ants seen on index cards. Ants were stored in 70 % ethanol and identified to species (or morphospecies) following keys, photos and taxonomy of Bolton (1994) and Longino (2009; 2011).

Data analyses

We examined differences between local and landscape characteristics of the three habitats (forest, high-, low-shade coffee) with two multivariate analyses of variance (MANOVA)—one for the 19 local and one for the seven landscape factors (Table 1). Significant

MANOVAs were followed by univariate ANOVAs and Tukey's post hoc tests to test for differences between habitats. We compared mean values for VCI and AI between habitats with ANOVA and Tukey's tests. Values for all variables were normally distributed.

We compared ant richness and abundance in the three habitats, and examined for relationships with VCI and AI. We defined ant abundance as the number of colonies, rather than individuals, to best examine community patterns. Because ants are colonial, chances of finding additional individuals drastically increases after finding the first, and using colonies for community level analysis is recommended (Ellison et al. 2007; Gotelli and Colwell 2001; Gotelli et al. 2011; Schlick-Steiner et al. 2006). We compared richness and abundance with ANOVA, and correlated ant species richness and colony abundance with the VCI and AI with linear and quadratic regressions (Gotelli and Ellison 2004). In order to select the best-fit model, we used the Akaike's information criterion (AIC) analysis computed with the 'MASS' package in R (R Development Core Team 2011; Venables and Ripley 2002). Because of the large number of regressions (16), we used a false discovery rate (FDR) adjusted α level for determining significance of each regression (Benjamini and Hochberg 1995). We conducted MANOVA, ANOVA, and regression analyses with SPSS v. 18.

To examine which local or landscape factors influenced ant richness and abundance we created conditional inference trees with the 'party' package in R (Hothorn et al. 2006; R Development Core Team 2011). Classification and regression trees examine the degree to which variables predict a dependent variable (Olden et al. 2008; Strobl et al. 2009), and can include variables with missing data, can determine the relative importance of individual factors, and allow setting a critical value for inclusion of variables rather than relying on pruning techniques. Conditional inference trees estimate relationships between variables by utilizing a binary recursive data-partitioning algorithm (Hothorn et al. 2006). The iterative process examines all variables searching for the best predictor of the dependent variable, splits the data into groups, and then repeats the variable selection until no more significant predictors are found. Because many local characteristics may be correlated, we attempted to reduce number of variables with a principal components analysis and Pearson correlations (Uno et al. 2010). However, most factors were not correlated with PC1 or PC2 ($P > 0.05$), so we used all 26 predictor variables in conditional inference trees (Table 1). We ran eight analyses, one for ant species richness and another for abundance for each of the four ant groups. We used the univariate option with a minimum criterion of 0.95 ($P < 0.05$).

In order to examine whether the proximity in sample plots or degree of overlap among buffer zones (Fig. 1) influenced the regression or conditional inference tree results, we tested for spatial autocorrelation in the dependent variables (Dormann et al. 2007). We examined the degree of spatial autocorrelation in the residuals of the regressions and conditional inference trees 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 2011). For the correlograms, we computed 100 permutations 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, we used nearest neighbor distances as the metric, and used the permutation test option. None of the variables examined for the regressions or the conditional inference trees displayed significant spatial autocorrelation at any distance (Table S2).

Table 1 Mean (\pm SE) values of local and regional characteristics, vegetation complexity index (VCI), agrochemical index (AI), and ant richness and abundance in forest, high-shade coffee, and low-shade coffee sites in a coffee landscape in Chiapas, Mexico

Habitat characteristics	Forest	High-shade	Low-shade	F [†]	P
VCI*	0.751 \pm 0.02 ^a	0.450 \pm 0.02 ^b	0.277 \pm 0.01 ^c	125.86	<0.001
AI*	0 ^b	0.163 \pm 0.66 ^b	0.598 \pm 0.51 ^a	34.576	<0.001
Local variables					
Herbicide use	0 ^b	0.384 \pm 0.14 ^b	1.29 \pm 0.14 ^a	26.158	<0.001
Fungicide use	0 ^b	0.384 \pm 0.14 ^b	1.47 \pm 0.15 ^a	32.159	<0.001
Pesticide use	0 ^b	0.15 ^b	0.71 ^a	13.74	<0.001
Fertilizer use	0 ^b	0.54 \pm 0.21 ^b	1.65 \pm 0.14 ^a	27.175	<0.001
Altitude (m)	1005.4 \pm 64.67	925.07 \pm 30.01	1047.70 \pm 44.11	1.974	0.153
Slope of terrain (°)	27.25 \pm 3.50	18.84 \pm 3.01	21.47 \pm 2.92	1.561	0.224
Leaf litter (g)	952.37 \pm 76.71 ^a	911.21 \pm 55.35 ^a	706.98 \pm 42.28 ^b	6.091	0.005
Humus (g)	1046.25 \pm 58.90	1034.94 \pm 40.04	960.80 \pm 55.93	0.809	0.453
No. tree species	35.30 \pm 4.09 ^a	9.31 \pm 3.60 ^b	5.12 \pm 1.14 ^b	29.266	<0.001
No. tree individuals	45.8 \pm 3.28 ^a	12.62 \pm 1.45 ^b	7.58 \pm 1.00 ^b	116.733	<0.001
Tree circumference (cm)	63.44 \pm 3.06 ^b	88.34 \pm 5.32 ^a	65.37 \pm 5.54 ^b	6.714	0.003
Tree height	15.08 \pm 1.03 ^a	12.27 \pm 1.08 ^a	6.74 \pm 0.73 ^b	21.142	<0.001
Canopy cover (%)	85.52 \pm 3.31 ^a	64.75 \pm 4.28 ^b	37.95 \pm 4.52 ^c	29.420	<0.001
No. coffee plants	0 ^c	117.69 \pm 8.01 ^b	165.29 \pm 5.76 ^a	168.74	<0.001
No. rotten logs per site	13.7 \pm 1.14	10.07 \pm 1.05	9.76 \pm 1.19	2.966	0.064
Rotten log length (cm)	197.11 \pm 17.16 ^a	169.97 \pm 19.60 ^a	91.95 \pm 9.59 ^b	13.772	<0.001
Rotten log circumference (cm)	37.46 \pm 2.31	43.18 \pm 2.39	46.01 \pm 3.81	1.600	0.216
Rotten log decay scale	2.91 \pm 0.04	2.88 \pm 0.09	2.62 \pm 0.17	1.366	0.268
No. hollow twigs*	NA	21.34 \pm 5.21	14.23 \pm 1.87	2.007	0.168
Landscape Variables					
Rustic coffee, 50 m (%)	0.97 \pm 0.97 ^{ab}	23.07 \pm 12.16 ^a	0 ^b	3.621	0.037
Rustic coffee, 200 m (%)	11.06 \pm 4.82	17.77 \pm 9.86	0.30 \pm 0.29	2.484	0.097
Rustic coffee, 500 m (%)	12.69 \pm 5.77	10.86 \pm 6.83	4.62 \pm 2.05	0.814	0.451
Forest, 50 m (%)	68.93 \pm 11.78 ^a	0 ^b	0.95 \pm 0.95 ^b	50.882	<0.001
Forest, 200 m (%)	40.79 \pm 7.36 ^a	3.99 \pm 2.34 ^b	2.12 \pm 1.57 ^b	31.087	<0.001
Forest, 500 m (%)	15.89 \pm 2.58 ^a	7.97 \pm 2.48 ^b	3.92 \pm 1.22 ^b	8.486	<0.001
Distance from forest (m)	0 ^b	407.23 \pm 84.69 ^a	452.52 \pm 72.03 ^a	10.386	<0.001
Ant variables*					
No. leaf litter colonies	35.7 \pm 2.92	33.61 \pm 2.96	27.35 \pm 2.82	2.260	0.119
No. leaf litter species	21.5 \pm 1.66	19.92 \pm 1.26	16.94 \pm 1.51	2.403	0.104
No. rotten log colonies	10.7 \pm 1.59	11.84 \pm 1.14	9.35 \pm 0.85	1.348	0.272
No. rotten log species	7.9 \pm 1.18	8.76 \pm 0.77	6.94 \pm 0.67	1.335	0.276
No. twig-nesting colonies	NA	13.61 \pm 2.86	14.76 \pm 2.61	0.010	0.920
No. twig-nesting species	NA	4.23 \pm 0.56	4.76 \pm 0.65	0.383	0.541
No. arboreal colonies	1.7 \pm 0.33 ^b	4.61 \pm 0.73 ^a	3.29 \pm 0.55 ^{ab}	4.976	0.012

Table 1 continued

Habitat characteristics	Forest	High-shade	Low-shade	F [†]	P
No. arboreal species	1.5 ± 0.30 ^b	3.84 ± 0.56 ^a	2.64 ± 0.43 ^{ab}	5.282	0.010

Values show mean and standard error. *Small letters* (a,b,c) show significant differences between treatments

* indicates the variable was compared between sites with univariate ANOVA

[†] $df = 2,37$ (except for hollow twigs, twig-nesting colonies and twig-nesting species where $df = 1, 28$)

Results

Site characteristics

Several local and landscape characteristics differed between habitat types (Table 1). Overall, local characters differed with habitat type ($F_{36,42} = 5.622$, $P < 0.001$). Factors that differed between habitat types included number of agrochemical applications, leaf litter weight, tree richness and tree abundance, tree circumference, tree height, canopy cover, number of coffee plants, and length of rotten logs (Table 1). Habitats did not differ for altitude, slope, humus, number of hollow twigs, or for the number, circumference or degree of decay of rotten logs. The VCI was higher in forest, an intermediate value in high-shade coffee, and lowest in low-shade coffee; all habitats significantly differed. AI differed between sites with significantly higher agrochemical use in the low-shade coffee compared with high-shade coffee or forest (Table 1). Landscape characteristics also differed with habitat ($F_{14,64} = 5.122$, $P < 0.001$) (Table 1). Distance from forest for high- and low-shade coffee sites did not differ, but forest sites were significantly closer to forest. At all scales examined (50, 200 and 500 m), there was more forest in the landscape for forest plots than for high- or low-shade coffee. Rustic coffee in the surrounding area only differed at the 50 m scale (Table 1).

Management effects on ant richness and abundance

We collected 16,991 ant individuals from ten subfamilies, 50 genera, and 115 morpho-species (Table S3). Ant richness and abundance differed between habitat types for arboreal ants, but not for the other groups. There were 2.7 times more arboreal ant colonies in the high-shade coffee than in forest, but arboreal ant abundance in high- and low-shade coffee, and in low-shade coffee and forest did not differ. Likewise, there were 2.6 times more arboreal ant species in high-shade coffee than in forests, but arboreal ant richness between high- and low-shade sites as well as in low-shade sites and forest sites did not differ. In contrast, there were no significant differences in species richness or abundance for leaf litter ants, ants that nest in rotten logs, or for arboreal twig-nesting ants (Table 1).

Species richness and colony abundance of most ant groups did not vary with vegetation complexity (VCI). There was no relationship between with vegetation complexity and the number of colonies of leaf litter ants ($y = 21.428x + 21.917$, $R^2 = 0.132$, $P_{FDR} = 0.084$), rotten log ants ($y = 2.994x + 9.164$, $R^2 = 0.018$, $P_{FDR} = 0.498$), arboreal twig-nesting ants ($y = 125.443x^2 - 166.754x - 6.350$, $R^2 = 0.1596$, $P_{FDR} = 0.221$) or arboreal tree trunk ants ($y = 21.659x^2 - 24.465x - 1.166$, $R^2 = 0.237$, $P_{FDR} = 0.056$). Species richness of leaf litter ants increased with increasing VCI ($y = 12.438x + 13.502$, $R^2 = 0.170$, $P_{FDR} = 0.043$). In contrast, there was no relationship between VCI and richness of rotten

log ants ($y = 2091x + 6.842$, $R^2 = 0.17$, $P_{FDR} = 0.490$), arboreal twig-nesting ants ($y = 33.133x^2 - 43.430x - 1.241$, $R^2 = 0.216$, $P_{FDR} = 0.121$) or arboreal tree trunk ants ($y = 21.606x^2 - 24.306x - 1.205$, $R^2 = 0.247$, $P_{FDR} = 0.080$).

Similarly, species richness and colony abundance of no group varied with agrochemical use (AI). There was no significant relationship between agrochemical use and numbers of colonies of leaf litter ants ($y = -8.072 + 33.955$, $R^2 = 0.055$, $P_{FDR} = 0.233$), rotten log ants ($y = -3.201x^2 + 201x + 11.483$, $R^2 = 0.61$, $P_{FDR} = 0.220$), twig-nesting ants ($y = -3.012x^2 + 6.052x + 4.118$, $R^2 = 0.101$, $P_{FDR} = 0.346$), or arboreal ants ($y = 1.814x^2 - 2.477x + 2.703$, $R^2 = 0.008$, $P_{FDR} = 0.968$). Richness of leaf litter ants ($y = -4.454 + 20.447$, $R^2 = 0.066$, $P_{FDR} = 0.216$), rotten log ants ($y = -3.028 + 8.705$, $R^2 = 0.101$, $P_{FDR} = 0.122$), twig-nesting ants ($y = -3.0102x^2 + 6.052x + 4.118$, $R^2 = 0.101$, $P_{FDR} = 0.317$), and arboreal ants ($y = 1.42x^2 - 1.957x + 2.695$, $R^2 = 0.005$, $P_{FDR} = 0.908$) did not vary with agrochemical use.

Influences of local and landscape characteristics on ant communities

Several factors significantly correlated with abundance and richness of different ant groups, and different groups responded to different local and landscape features. Ant abundance was best predicted by local factors, with only one ant group correlating with one landscape factor (Fig. 2). The number of leaf litter colonies was higher with greater humus mass, with more forest area within 200 m of the study site, and where logs were more decayed (Fig. 2a). The number of colonies of ants nesting in rotten logs was not correlated with any factor (Fig. 2b). The number of twig-nesting ant colonies was higher with more hollow twigs (Fig. 2c). The number of arboreal ant colonies was higher with trees with larger circumference (Fig. 2d). Richness of three groups was more strongly predicted by local factors, and one group responded to a landscape factor. Leaf litter ant richness was higher with more humus, with more forest area within 200 m, and with larger tree circumference (Fig. 3a). Richness of ants that nest in rotten logs was lower where fertilizers were applied (Fig. 3b). Richness of twig-nesting species was higher more distant from the forest fragments (Fig. 3c). Arboreal ant richness was higher with higher tree circumference (Fig. 3d).

Discussion

Ants, habitat, and management

One question we addressed is whether ant abundance and richness differs in forests and coffee farms of varying management intensity. Coffee management intensity can be characterized in several ways including differences in arboreal vegetation. Our three habitat types (forest, high-shade coffee, and low-shade coffee) differed in terms of several vegetation characteristics and the VCI. Compared with the habitat categories, the VCI more specifically tracks the vegetation characteristics of each site and thus may monitor a more precise change in the related ant communities. However, neither differences in habitat or the VCI strongly related to changes in ant richness or abundance. Below we discuss relationships between habitat type and VCI and different groups of ants.

Of those ants sampled on the ground, only leaf litter ant richness increased with VCI; there were no differences in richness of leaf litter ants or ants in rotten logs between different habitat types, or significant correlations between leaf litter ant abundance or

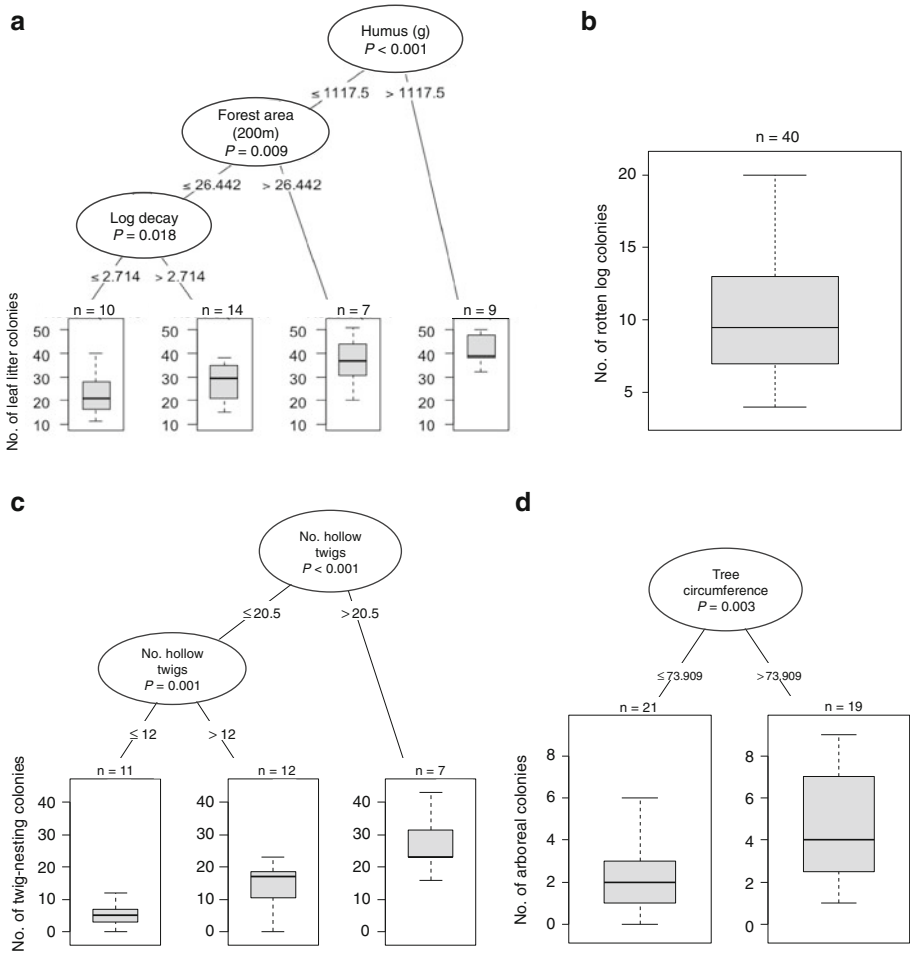


Fig. 2 Conditional inference trees examining relationships between 19 local and seven regional factors and number of ant colonies for: **a** leaf litter, **b** rotten log, **c** twig-nesting and **d** arboreal ants. Predictor variables are circled and ranked (top, highest correlation with dependent variable). *P*-values indicate the significance of the relationship being tested. Box plots include the inner quartiles (grey 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

rotten log ant richness or abundance with VCI. Sites with a more complex vegetation structure may produce more litter and humus (Armbrecht et al. 2005; Schonberg et al. 2004). This, in turn, could alter soil and litter-dwelling invertebrate communities and reduce litter decomposition rate, thereby affecting litter ant abundance and richness (Vasconcelos and Laurance 2005). Our results are consistent with other studies investigating leaf litter ants in coffee farms in that leaf litter ant diversity and abundance generally decline with more intensive shade management schemes (Bisseleua et al. 2009; Perfecto and Snelling 1995; Perfecto and Vandermeer 2002). We did not find differences in richness or abundance of ants nesting in rotten logs in different habitats or with variation in VCI. This result is consistent with De la Mora and Philpott (2010) who sampled seasonal

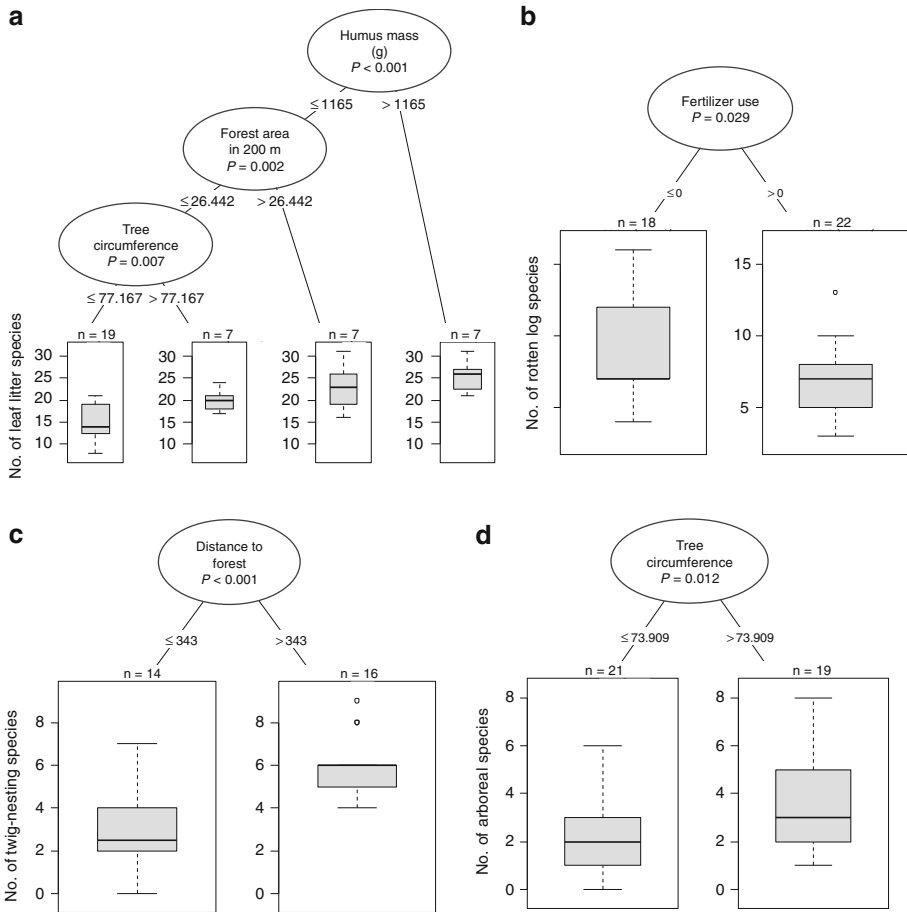


Fig. 3 Conditional inference trees examining relationships between 19 local and seven regional factors and number of ant species for: **a** leaf litter, **b** rotten log, **c** twig-nesting and **d** arboreal ants. Explanation is as for Fig. 2

variation and coffee management impacts on ants in rotten logs in a small subset of coffee farms included in this study during a different sample year. They argued that one potential reason why ant abundance and richness did not differ is because in more intensively managed coffee farms, shade trees are heavily pruned, and some logs may be left on the ground, increasing nesting sites for this guild of ant.

Of those ants sampled on vegetation, tree trunk ant abundance and richness were higher in high-shade coffee than in low-shade coffee, but abundance and richness of arboreal ants did not differ with VCI. Further, twig-nesting ant abundance and richness did not differ with habitat type or with changes in the VCI. There are a few reasons for why arboreal, tree-trunk ant richness and abundance was higher in the high-shade sites, compared with forest or low-shade sites. First, in forest sites, there may be more abundant resources in the canopy including extrafloral nectaries, hemipteran resources, and prey that may retain ants in the canopy (Blüthgen et al. 2004; Davidson et al. 2003; Kaspari and Yanoviak 2001). As such, baits for arboreal ants on tree trunks may not have been attractive or efficient for

collecting the truly arboreal ants (Schonberg et al. 2004). Second, in high-shade sites, there may have been more ants foraging lower in the canopy, the coffee layer, or even on the ground in order to obtain ample resources for colony maintenance and growth (Batáry et al. 2010). Third, diversity may be higher with intermediate frequency and intensity of disturbances (Connell 1978), and shade trees experience regular pruning (a disturbance) which may have increased densities of arboreal ants lower in the canopy in the high-shade sites (Philpott 2005).

Intensity of agrochemical use is also an indicator of coffee management intensity. However, agrochemical use was not correlated with any changes in abundance or richness of the four ant groups examined. These results are consistent with other studies that failed to find that ant communities respond to pesticide gradients (Chong et al. 2007; Matlock and de la Cruz 2003). However chemical residues alter chemical properties of the soil and soil microflora (Petal 1980) and have negative effects on not-target organisms like ants (Matlock and de la Cruz 2003). We propose two reasons why agrochemicals did not affect abundance and richness of ants in this study. First, ant sampling was not conducted on the same days that agrochemicals were applied and sensitivity of an organism to a particular pesticide depends on toxicity and probability of exposure (Chong et al. 2007). In addition, some of the ants collected (e.g. twig-nesting ants) may have been protected from agrochemicals during spraying, due to their specific foraging or nesting patterns.

Ants and local and landscape factors

We also aimed to determine which local and landscape level characteristics correlate with abundance and richness of different ant groups. According to conditional inference trees, most factors that correlated with ant richness or abundance were local factors. However, litter and twig-nesting ant richness and abundance was affected by landscape factors. Below, we discuss the significant predictive variables for each ant group, and offer explanations for how the local and landscape factors may interact.

Leaf litter ant abundance increased with humus mass, area of forest within 200 m, and with increasing degree of log decay. Richness was related to humus mass, area of forest within 200 m, and with increasing tree circumference. The most important predictor of richness and abundance was humus that provides important microhabitat and nutrients for the microbial community (Rivera and Armbrrecht 2005; Vasconcelos and Laurance 2005). Humus mass correlates with litter depth, documented as an important predictor of tropical leaf litter ant communities, especially when correlated with both ample food and nesting resources (Kaspari 1996; Shik and Kaspari 2010). Leaf litter ant richness is often higher closer to forest (Armbrrecht and Perfecto 2003; Carvalho and Vasconcelos 1999; Perfecto and Vandermeer 2002) or in sites with higher percentage of forest at 50 and 200 m scales (Dauber et al. 2003).

Application of synthetic fertilizers correlated with decreased abundance of ants collected from rotten logs. Likely, this is due to either direct effects of fertilizers on ant mortality, or indirect effects due to changes in the abundance of microflora in the soil or logs (Petal 1980). Microbiotic conditions in the litter could affect ground-dwelling ants in two different ways. First, changes in microfauna abundance or diversity, temperature, chemical conditions, or litter humidity could alter activity of ants that live or reproduce under certain microhabitat conditions (Byrne 1994; Clergue et al. 2005; Kaspari and Weiser 2000; Rivera and Armbrrecht 2005). Second, ants nesting in rotten logs are frequently considered specialists that feed on small, relatively abundant insects such as collembolans, bristletails, millipedes, and termites (Brown 1976; Davidson et al. 2003;

Hölldobler and Wilson 1990; Longino 2011). Fertilizer application can change soil pH, thereby changing abundance and composition of mite and springtail communities (Oliver et al. 2005). Furthermore, application of synthetic fertilizers may eliminate ammonifying bacteria, resulting in a decrease in the abundance of microflora, which could change the chemical characteristics of the soil (Oliver et al. 2005; Petal 1980). Changes in the microbial community in the soil, litter, or in the rotting logs may affect potential prey resources for this guild of ants (Brown 1976).

The number of twig-nesting ant colonies was correlated with the number of hollow twigs, and richness was negatively correlated with distance from forest. Nest site limitation increases where nest availability is low and limits abundance of twig-nesting ants (Armbrrecht et al. 2005; Philpott and Foster 2005). Distance from forest was the only factor that influenced twig-nesting ant richness. This was an unexpected result as most studies on ants document decreases (not increases) with distance to forest because of dispersal limitation, or a lack of forest-based resources far from fragments (e.g. Armbrrecht and Perfecto 2003; Perfecto and Vandermeer 2002). However, distance from forest was positively correlated with number of hollow twigs ($y = 0.023 + 7.349x$, $R^2 = 0.247$, $P = 0.006$), and may largely account for this pattern.

The single predictive factor for arboreal ant richness and abundance was tree circumference. Tree characteristics (e.g. shade cover and tree density) are important for maintaining richness and abundance of arboreal guild (Kaspari and Weiser 2000; Philpott and Foster 2005), and as tree circumference is smaller, trees tend to be smaller limiting the number of available resources in the canopy. Many tropical arboreal ants forage extensively for herbivores and insect secretions in the canopy, and any differences in canopy structure may alter available resources (Davidson et al. 2003; Hahn and Wheeler 2002). Interestingly, a recent paper documented that species richness of tropical arboreal ants in primary and secondary forests (in Papua New Guinea) is most strongly influenced by nest availability, rather than taxonomic diversity or a loss of specific types of resources (e.g. epiphytes, nectaries, etc.) (Klimes et al. 2012). Trees with larger circumference may indeed offer more nest sites for ants and could be one possible explanation for this result.

Local and landscape influences on ants

Finally, we aimed to determine whether ants primarily respond to changes in local or landscape characteristics. Overall, ants responded strongly and more frequently to local rather than landscape factors, consistent with previous studies on ants in managed landscapes (Bestelmeyer and Wiens 1996; Dauber et al. 2005). For example, some studies comparing local and landscape influences on ants note that habitat characteristics like insolation and soil conditions more strongly affect ant communities than landscape factors (Dauber et al. 2005). We found two landscape factors that were important for two ant groups. First, distance from forest negatively correlated with twig-nesting ant richness and abundance. Distance to forest was positively correlated with the abundance of hollow twigs, likely a stronger factor for twig-nesting ant communities. Other landscape characteristics measured were not strong predictors of ant richness or abundance in this coffee landscape. Second, richness and abundance of leaf litter ants were related to the amount of forest with 200 m, a result confirming previous studies.

One reason that ants respond to local characteristics may be their low mobility, but even very mobile organisms are affected by local factors. Other not so mobile (e.g. Diplopoda), and even some highly mobile organisms (e.g. Staphylinidae) show limited responses to landscape changes (Dauber et al. 2005). In addition, richness of bees, highly mobile

organisms, in coffee landscapes is more affected by tree richness, diversity of flowering trees, and canopy cover than distance from forest and amount of diverse shade coffee habitat nearby (Jha and Vandermeer 2010). Bird richness in Costa Rican coffee landscapes was more strongly affected by higher richness and abundance of trees than distance to forest reserves (Daily et al. 2001). In contrast, Ricketts et al. (2001) found that although moth richness was not related to amount of forest within 500 m, forest within 800 m did positively correlate with moth richness. It is possible that the 500 m spatial extent in our study may have not been sufficient to capture landscape influences. However, this distance was large enough to detect influences of landscape variables on ant communities in other systems (Dauber et al. 2005). In addition, the relative importance of local and landscape factors may depend on the landscape context. For example, Tschamtkke et al. (2012) suggest that local factors are more important in simple landscapes and local effects diminish as landscape complexity increases. In the study region, most of the landscape is coffee (~94 %), or a simple landscape according to the threshold outlined by Tschamtkke et al. (2012). Thus we could expect there to be strong influence of local factors.

Conclusions and conservation implications

This work presents novel data investigating multiple characteristics of agroecosystems and the surrounding landscape and their effects on abundance and richness of four ant groups. Additionally, this is the first study to quantitatively assess the impacts of agrochemical use on ant communities in coffee agroecosystems. Ultimately, the goal of this study is to relate the results to promote ant conservation in coffee landscapes, and specifically, to determine which local and landscape factors contribute most to community level patterns for a diverse group of tropical organisms. We found that mainly local level factors affect the diversity and abundance of ants, but that each guild responds differently to certain management aspects. Because many of these ants are biological control agents, farm management decisions may have direct impacts on ecosystem services provided by ants in coffee landscapes. Importantly, relationships between ant abundance and richness and vegetation complexity here were often not linear. Some studies assume direct, linear tradeoffs between production and biodiversity, but other authors (Perfecto et al. 2005; Steffan-Dewenter et al. 2007) find non-linear tradeoffs. Thus, there is the possibility that conservation goals (protecting ant richness) and production goals (increasing pest control services, and promoting yield) may be more compatible than assumed.

Acknowledgments A. García Ballinas, J. Santis, G. Dominguez, U. Pérez Vásquez, G. López Bautista, B.E. Chilel, E. Schüller, S. Arming, and E. Sintes assisted with field work. R. Becker, R. John, and J.H. López Urbina assisted with the GIS analysis. B. Nickel provided assistance with spatial analysis. G. Ibarra Núñez, J. Rojas, J. Valle-Mora, and E. Chamé Vásquez of El Colegio de la Frontera Sur (ECOSUR) provided logistical support. C. Hochreiter, D. Gonthier, K. Ennis, G. Ibarra Núñez, J.-P. Lachaud, G. Pérez-Lachaud, L. Soto-Pinto, D. Allen, D. Jackson and J. Remfert provided comments on the manuscript. We thank the owners of Fincas Irlanda, Argovia, Hamburgo, San Francisco, Genova, Rancho Alegre, Chiripa, Maravillas, Santa Anita, San Enrique and the Rogers Family Company for allowing us to conduct research on their farms. Finca Irlanda and Don Walter Peters provided housing. CM was funded by University of Toledo Undergraduate Summer Research and Creative Activity Program, A Study Abroad Travel Grant, and the Explorer's Club Youth Activity Fund. ADM was funded by scholarship number 168970 granted by the National Council of Science and Technology (CONACYT) in Mexico and a Conservation International Rapid Assessment Program award. Additional funding was provided by NSF DEB-1020096 to SMP.

References

- Agosti D, Alonso LE (2000) The ALL Protocol, a standard protocol for the collection of ground-dwelling ants. In: Agosti D, Majer JD, Alonso LE, Shultz TR (eds) *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution, Washington, DC, pp 204–206
- Andersen AN, Majer JD (2004) Ants show the way down under: invertebrates as bioindicators in land management. *Front Ecol Environ* 2:291–298
- Andersen AN, Hoffmann BD, Muller WJ, Griffiths AD (2002) Using ants as bioindicators in land management: simplifying assessment of ant community responses. *J Appl Ecol* 39:8–17
- Armbrecht I, Perfecto I (2003) Litter-twig dwelling ant species richness and predation potential within a forest fragment and neighboring coffee plantations of contrasting habitat quality in Mexico. *Agric Ecosyst Environ* 97:107–115
- Armbrecht I, Rivera L, Perfecto I (2005) Reduced diversity and complexity in the leaf-litter ant assemblage of Colombian coffee plantations. *Conserv Biol* 19:897–907
- Batáry P, Matthiesen T, Tscharnke T (2010) Landscape-moderated importance of hedges in conserving farmland bird diversity of organic versus conventional croplands and grasslands. *Biol Conserv* 143:2020–2027
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J R Stat Soc* 57:289–300
- Bestelmeyer BT, Wiens JA (1996) The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. *Ecol Appl* 6:1225–1240
- Bestelmeyer BT, Agosti D, Alonso LE, Brandão CRF, Brown WL, Delabie JHC, Silvestre R (2000) Field techniques for the study of ground-dwelling ants. In: Agosti D, Majer JD, Alonso LE, Shultz TR (eds) *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution, Washington, DC, pp 122–144
- Bianchi FJ, Booij CJ, Tscharnke T (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc R Soc B* 273:1715–1727
- Bisseleua DHB, Missoum AD, Vidal S (2009) Biodiversity conservation, ecosystem functioning, and economic incentives under cocoa agroforestry intensification. *Conserv Biol* 23:1176–1184
- Bivand R, Altman M, Anselin L, Assunção R, Berke O, Bernat A, Blanchet G, Blankmeyer E, Carvalho M, Christensen B, Chun Y, Dormann C, Dray S, Halbersma R, Krainski E, Legendre P, Lewin-Koh N, Li H, Ma J, Millo G, Mueller W, Ono H, Peres-Neto P, Piras G, Reder M, Tiefseldorf M, Yu D (2012) *spdep: Spatial dependence: weighting schemes, statistics and models*. R package version 0.5-46. <http://CRAN.R-project.org/package=spdep>. Accessed Dec 2012
- Bjornstad O (2009). *nfc: spatial nonparametric covariance functions*. R package version 1.1-3. <http://CRAN.R-project.org/package=nfc>. Accessed Dec 2012
- Blüthgen N, Stork NE, Fiedler K (2004) Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. *Oikos* 106:344–358
- Bolton B (1994) *Identification guide to the ant genera of the world*. Harvard University Press, Cambridge
- Brown WL Jr (1976) Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section A. Introduction, subtribal characters. *Genus Odontomachus Stud Entomol* 19:167–171
- Byrne MM (1994) Ecology of twig-dwelling ants in wet lowland tropical forest. *Biotropica* 6:61–72
- Carvalho KS, Vasconcelos HL (1999) Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. *Biol Conserv* 91:151–157
- Castellon T, Sieving K (2006) An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conserv Biol* 20:135–145
- Chong CS, Hoffmann AA, Thomson LT (2007) Commercial agrochemical applications in vineyards do not influence ant communities. *Environ Entomol* 36:1374–1383
- Clergue B, Amiaud B, Pervanchon F, Lasserre-Joulin F, Plantureux S (2005) Biodiversity: function and assessment in agricultural areas A review. *Agron Sustain Dev* 25:1–15
- Concepción EC, Díaz M, Baquero RA (2008) Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. *Landsc Ecol* 23:135–148
- Connell JH (1978) Diversity in tropical rain forest and coral reefs. *Science* 199:1302–1310
- Daily GC, Ehrlich PR, Sánchez-Azofeifa A (2001) Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecol Appl* 11:1–13
- Dauber J, Hirsch M, Simmering D, Waldhardt R, Otte A, Wolters V (2003) Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agric Ecosyst Environ* 98:321–329

- Dauber J, Purtauf T, Allspach A, Frisch J, Voigtländer K, Wolters V (2005) Local versus landscape controls on diversity: a test using surface-dwelling soil macroinvertebrates of differing mobility. *Global Ecol Biogeogr* 14:213–221
- Davidson DW, Cook SC, Snelling RR, Chua TH (2003) Explaining the abundance of ants in lowland tropical rainforest canopies. *Science* 300:969–972
- De la Mora A, Philpott SM (2010) Wood-nesting ants and their parasites in forests and coffee agroecosystems. *Environ Entomol* 39:1473–1481
- Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FM, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30:609–628
- Duffy JE (2009) Why biodiversity is important to the functioning of real-world ecosystems. *Front Ecol Environ* 7:437–444
- Ellison AM, Record S, Arguello A, Gotelli NJ (2007) Rapid inventory of the ant assemblage in a temperate hardwood forest: species composition and assessment of sampling methods. *Environ Entomol* 36:766–775
- Gabriel D, Sait SM, Hodgson JA, Schmutz U, Kunin WE, Benton TG (2010) Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecol Lett* 13:858–869
- García Estrada C, Damon A, Sánchez Hernández C, Soto Pinto L, Guillermo Ibarra-Núñez G (2006) Bat diversity in montane rainforest and shaded coffee under different management regimes in southeastern Chiapas, Mexico. *Biol Conserv* 132:351–361
- Gibb H, Hjältén J, Ball JP, Atlegrim O, Pettersson RB, Hilszczanski J, Johansson T, Danell K (2006) Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. *Ecography* 29:191–204
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391
- Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer Associates, Inc., Sunderland
- Gotelli NJ, Ellison AM, Dunn RR, Sanders NJ (2011) Counting ants (Hymenoptera: formicidae): biodiversity sampling and statistical analysis for myrmecologists. *Myrmecol News* 15:13–19
- Hahn D, Wheeler DE (2002) Seasonal foraging activity and bait preferences of ants on Barro Colorado Island, Panama. *Biotropica* 34:348–356
- Hoffmann BD (2010) Using ants for rangeland monitoring: global patterns in the responses of ant communities to grazing. *Ecol Indic* 10:105–111
- Hölldobler B, Wilson EO (1990) *The Ants*. Springer, Berlin
- Hothorn T, Hornik K, Zeileis A (2006) Unbiased recursive partitioning: a conditional inference framework. *J Comput Graph Stat* 15:651–674
- Jha S, Vandermeer JH (2010) Impacts of coffee agroforestry management on tropical bee communities. *Biol Conserv* 143:1423–1431
- Jules E, Shahani P (2003) A broader ecological context to habitat fragmentation: why matrix habitat is more important than we thought. *J Veg Sci* 14:459–464
- Kaspari M (1996) Testing resource-based models of patchiness in four neotropical litter ant assemblages. *Oikos* 76:443–454
- Kaspari M, Weiser MD (2000) Ant activity along moisture gradients in a neotropical forest. *Biotropica* 32:703–711
- Kaspari M, Yanoviak SP (2001) Bait use in tropical litter and canopy ants—evidence of differences in nutrient limitation. *Biotropica* 33:207–211
- Klimes P, Idigel C, Rimandai M, Fayle TM, Janda M, Weiblen GD, Novotny V (2012) Why are there more arboreal ant species in primary than in secondary tropical forests? *J Anim Ecol* 81:1103–1112
- Longino JT (2009) Additions to the taxonomy of New World *Pheidole* (Hymenoptera: formicidae). *Zootaxa* 2181:1–90
- Longino JT (2011) Ants of Costa Rica. <http://academic/evergreen.edu/projects/ants/AntsofCostaRica.html>. Accessed January, 2011
- Matlock RB, de la Cruz R (2003) Ants as indicators of pesticide impacts in banana. *Environ Entomol* 32:816–829
- McGlynn T, Fawcett R, Clark D (2009) Litter biomass and nutrient determinants of ant density, nest size, and growth in a Costa Rican tropical wet forest. *Biotropica* 2:234–240
- Moguel P, Toledo V (1999) Biodiversity conservation in traditional coffee systems of Mexico. *Conserv Biol* 13:11–21
- Moorhead LC, Philpott SM, Bichier P (2010) Epiphyte biodiversity in the coffee agricultural matrix: canopy stratification and distance from forest fragments. *Conserv Biol* 24:737–746

- Økland B, Bakke A, Hagvar S, Kvamme T (1996) What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiv Conserv* 5:75–100
- Olden JD, Lawler JJ, Poff NL (2008) Machine learning methods without tears: a primer for ecologists. *Q Rev Biol* 83:171–192
- Oliver I, Garden D, Greenslade PJ, Haller B, Rodgers D, Seeman O, Johnston B (2005) Effects of fertiliser and grazing on the arthropod communities of a native grassland in south-eastern Australia. *Agric Ecosyst Environ* 109:323–334
- Peck SL, McQuaid B, Lee C (1998) Using ant species (Hymenoptera: formicidae) as a biological indicator of agroecosystem condition. *Environ Entomol* 27:1102–1110
- Perfecto I, Snelling R (1995) Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. *Ecol Appl* 5:1084–1097
- Perfecto I, Vandermeer J (1996) Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. *Oecologia* 108:577–582
- Perfecto I, Vandermeer J (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in Southern Mexico. *Conserv Biol* 16:174–182
- Perfecto I, Rice R, Greenberg R, Van der Voort M (1996) Shade coffee: a disappearing refuge for biodiversity. *Bioscience* 46:598–608
- Perfecto I, Vandermeer J, Mas A, Soto Pinto L (2005) Biodiversity, yield, and shade coffee certification. *Ecol Econ* 54:435–446
- Petal J (1980) Ant populations, their regulation and effect on soil in meadows. *J Pol Sci* 28:297–326
- Philpott SM (2005) Changes in arboreal ant populations following pruning of coffee shade-trees in Chiapas, Mexico. *Agroforest Syst* 64:219–224
- Philpott SM, Foster PF (2005) Nest-site limitation in coffee agroecosystems: artificial nests maintain diversity of arboreal ants. *Ecol Appl* 5:1478–1485
- Philpott SM, Arendt W, Armbrrecht I, Bichier P, Dietsch T, Gordon C, Greenberg R, Perfecto I, Soto-Pinto L, Tejada-Cruz C, Williams G, Valenzuela J (2008a) Biodiversity loss in Latin American coffee landscapes: reviewing evidence on ants, birds, and trees. *Conserv Biol* 22:1093–1105
- Philpott SM, Lin BB, Jha S, Brines SA (2008b) A multi-scale assessment of hurricane impacts based on land-use and topographic features. *Agric Ecosyst Environ* 128:12–20
- R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org/>
- Ricketts T, Daily G, Ehrlich P, Fay J (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conserv Biol* 15:378–388
- Rivera L, Armbrrecht I (2005) Diversidad de tres gremios de hormigas en cafetales de sombra, de sol y bosques de Risaralda. *Rev Colomb Entomol* 31:89–96
- Schlick-Steiner BC, Steiner FM, Moder K, Bruckner A, Fiedler K, Christian E (2006) Assessing ant assemblages: pitfall trapping versus nest counting (Hymenoptera, Formicidae). *Insect Soc* 53:274–281
- Schmidt MH, Thies C, Nentwig W, Tscharrntke T (2008) Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *J Biogeogr* 35:157–166
- Schonberg LA, Longino J, Nadkarni NM, Yanoviak SP, Gering J (2004) Arboreal ant species richness in primary forest, secondary forest, and pasture habitats of a tropical montane landscape. *Biotropica* 36:402–440
- Shik JZ, Kaspari M (2010) More food, less habitat: how necromass and leaf litter decomposition combine to regulate a litter ant community. *Ecol Entomol* 35:158–165
- Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharrntke T (2002) Scale dependent effects of landscape context on three pollinator guilds. *Ecology* 83:1421–1432
- Steffan-Dewenter I, Kessler M, Barkmann J, Bos MM, Buchori D, Erasmi S, Faust H, Gerhold G, Glenk K, Grandstein SR, Guhardja E, Harteveld M, Hertel D, Höhn P, Kappas M, Köhler S, Leuschner C, Maertens M, Marggraf R, Migge-Kleian S, Mogeia J, Pitopang R, Schaefer M, Schwarze S, Sporn SG, Steingrebe A, Tjitrosoedirdjo SS, Tjitrosoemito S, Twele A, Weber R, Woltmann L, Zeller M, Tscharrntke T (2007) Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proc Natl Acad Sci* 104:4973–4978
- Strobl C, Hothorn T, Zeileis A (2009) Party on! *The R Journal* 2:14–17
- Teodoro AV, Sousa-Souto L, Klein AM, Tscharrntke T (2010) Seasonal contrasts in the response of coffee ants to agroforestry shade-tree management. *Environ Entomol* 39:1744–1750
- Torres JA (1994) Wood decomposition of *Cyrrilla racemiflora* in a tropical montane forest. *Biotropica* 26:124–140
- Tscharrntke T, Klein A, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol Lett* 8:857–874

- Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Steffan-Dewenter I, Thies C, van der Putten WH, Westphal C (2012) Landscape moderation of biodiversity patterns and processes—eight hypotheses. *Biol Rev Camb Philos Soc* 87:661–685
- Tylianakis JM, Klein AM, Tscharntke T (2005) Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology* 86:3296–3302
- Uno S, Cotton J, Philpott SM (2010) Diversity and species composition of ants in urban green spaces. *Urban Ecosyst* 13:425–441
- Vandermeer J, Carvajal R (2001) Metapopulation dynamics and the quality of the matrix. *Am Nat* 159:211–220
- Vasconcelos HL, Laurance WF (2005) Influence of habitat, litter type, and soil invertebrates on leaf-litter decomposition in a fragmented Amazonian landscape. *Oecologia* 144:456–462
- Venables WN, Ripley BD (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York. ISBN 0-387-95457-0