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## Ant patchiness: a spatially quantitative test in coffee agroecosystems

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**Abstract** Arboreal ants form patchy spatial patterns in tropical agroforest canopies. Such patchy distributions more likely occur in disturbed habitats associated with lower ant diversity and resource availability than in forests. Yet, few studies have quantitatively examined these patchy patterns to statistically test if ants are non-randomly distributed or at what scale. Coffee agroecosystems form a gradient of management intensification along which vegetative complexity and ant diversity decline. Using field studies and a spatially explicit randomization model, I investigated ant patchiness in coffee agroecosystems in Chiapas, Mexico varying in management intensity to examine if: (1) coffee intensification affects occurrence of numerically dominant ants, (2) numerical dominants form statistically distinguishable single-species patches in coffee plants, (3) shade trees play a role in patch location, and (4) patch formation or size varies with management intensity. Coffee intensification correlated with lower occurrence frequency of numerically dominant species generally and of one of four taxa examined. All dominant ant species formed patches but only *Azteca instabilis* was patchy around shade trees. Ant patchiness did vary somewhat with spatial scale and with strata (within the coffee layer vs around shade trees). Patchiness, however, did not vary with management intensity. These results provide quantitative evidence that numerically dominant ants are patchy within the coffee layer at different scales

and that shade tree location, but not coffee management intensity, may play a role in the formation of patchy distributions.

### Introduction

In tropical agroforests, numerically dominant ants, those found in higher numbers, biomass, or frequency of occurrence, are often spatially arranged such that different species may form mutually exclusive patches where submissive ants coexist (Leston 1973; Room 1975; Majer 1978; Majer and Queiroz 1993; Davidson 1998). Descriptions of these patchy patterns, although abundant in the literature, are mostly qualitative; researchers generally use maps to show patchy distributions without quantifying spatial patterns (e.g., Leston 1973; Majer and Queiroz 1993). Many non-exclusive hypotheses explain formation of patchy distribution patterns including (1) interspecific competition (Leston 1973; Room 1975; Majer 1978; Adams 1994), (2) stochastic processes (Ribas and Schoereder 2002), (3) decreasing species richness (Hölldobler and Wilson 1990), (4) physical or temporal habitat specialization (Floren and Linsenmair 2000; Soares and Schoereder 2001), and (5) anthropogenic disturbances (Floren et al. 2001). Ants are more likely patchily distributed in disturbed habitats where they suffer more intense resource competition for food or nest sites (Floren and Linsenmair 2000; Floren et al. 2001). In this paper, I quantitatively test for patchy distributions of ants in the coffee plant layer of coffee agroecosystems to examine if these patterns are statistically distinguishable from random and if patchiness is related to shade tree locations or influenced by coffee management intensity.

Coffee agroecosystems fall along an intensification gradient from those cultivated under a native forest shade canopy at the least intensive end, towards intensive production characterized by lower density, diversity, and height of shade trees, lower canopy cover, higher coffee density, and agrochemical use (Moguel and Toledo 1999). Generally speaking, coffee intensification results in losses

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of ant biodiversity (Philpott and Armbrrecht 2006), but this is not always the case (Lachaud and García-Ballinas 2001). Diversity losses are likely a result of microclimatic differences (Perfecto and Vandermeer 1996), reductions in number or diversity of nesting sites (Armbrrecht et al. 2004), or increases in pesticide use. In shaded coffee agroecosystems, numerically dominant arboreal ants most often nest in shade trees and forage in coffee plants nearby (Vandermeer et al. 2002), only sometimes nesting in coffee plants. Although most studies examining the patchy distributions of ants refer to ant communities in canopy trees, it is likely that, where fewer trees are available as nest sites, patchy distributions may form in what is usually the understory—i.e., the coffee plant layer. Furthermore, given that patchy patterns are influenced by habitat disturbance and that trees play an important role in arboreal ant communities, coffee management intensification may affect distributions of patch-forming arboreal ants within the coffee agroecosystems.

In this study, I quantitatively tested for single-species patches of numerically dominant arboreal ants in the coffee plant layer (excluding the shade canopy) and examined whether shade tree locations or management intensification may affect either location or size of patches in coffee farms. I specifically asked (1) whether coffee intensification affects occurrence frequency of numerical dominants, (2) if numerical dominants form statistically distinguishable single-species patches in the coffee layer, (3) if shade tree location plays a role in the placement of patches, and (4) if the number of species forming patches or if size of patches varies with management intensity. The approach here is relatively new in that it uses a quantitative model to test for ant patchiness, thereby allowing us to statistically distinguish single-species patches in a landscape and also allowing quantitative testing of alternative hypotheses for formation of patchy distributions (but see Theunis et al. 2005, for a review).

## Materials and methods

### Site description

I carried out field studies in four farms in the Soconusco region of SW Chiapas, Mexico: (1) Finca Belen (15°15' N, 92°22' W), (2) Finca Irlanda (15°11' N, 92°20' W), (3) Finca Hamburgo (15°10' N, 92°19' W), and (4) Guadalupe Zajú (15°9' N, 92°17' W). All farms cover more than 200 ha and receive ca. 4,500 mm of rain per year, and all study plots within farms are located between 950 and 1,150 m. According to the coffee management scheme of Moguel and Toledo (1999) and in order of increasing intensification, Irlanda and Belen both contain areas of traditional polyculture and commercial polyculture, Hamburgo is a shaded monoculture, and Guadalupe Zajú is an unshaded sun plantation. Irlanda and Belen are both certified organic farms and no pesticides have been used in Hamburgo for at least 5 years. Guadalupe Zajú was also the only site where pesticides may have been used but this

information was not made available to me. Coffee densities varied between sites but, in general, plants are separated by 0.5–3 m and sometimes are directly touching other coffee plants or shade trees. I haphazardly established a total of nine 25×50-m survey plots in the four farms to capture the range of management intensification. I set up three plots in traditional polycultures (TPB1, TPB2, and TPI), three in commercial polycultures (CPB1, CPB2, and CPI), two in shade monocultures (SM1 and SM2), and one in unshaded sun production (SUN). I established six of them in June 2000 (TPB1, TPI, CPB1, CPI, SM1, and SM2), two of them in January 2001 (TPB2 and CPB2), and the final one in June 2002 (SUN).

### Vegetation and ant sampling

To verify the qualitative assessments of management intensity in each plot, I surveyed multiple vegetation characteristics and summarized these using a management index. I collected data on percent shade cover, shade tree density, tree species richness, number of trees >100 cm circumference at breast height, and coffee density. I estimated percent cover for all sites in January 2001, June 2001, January 2002, and June 2002 using a vertical tube densitometer. Every 5 m throughout plots, for a total of 50 points, I recorded 0, 50, or 100% cover and averaged all points for a per-plot value. I summarized all vegetation variables using a management index (modified from Mas and Dietsch 2003). Raw data for each variable (per plot and per date) were converted to a scale from 0 (least intensive) to 1 (most intensive). To convert all variables except coffee density, I divided each measurement by the highest possible value and subtracted by one. Increases in coffee density, unlike increases of the remaining vegetation variables, correspond to increasing management intensity. Thus, for coffee density, I divided by the lowest measurement and subtracted by one. I summed values for each variable for a possible total of five per plot and divided by the number of variables measured on each date.

I surveyed coffee plants and shade trees for foraging ants in most plots three times in the wet season (June 2000, 2001, and 2002) and twice in the dry season (January 2001 and 2002), depending on the date in which plots were established. All ants were sampled during the day, thus no nocturnally foraging ants were included in the study. In each plot, I first mapped *x*- and *y*-coordinates of coffee and shade trees. I sampled ants in each coffee plant by kicking or shaking plants and watching branches, leaves, and trunks for 2 min after disturbances. I sampled shade trees using tuna baits (5–10 g) placed on trunks 1 m above-ground and checked after 30–45 min. Coffee plants and shade trees were assigned to the following categories based on the presence of foraging workers: (1) *Azteca instabilis* (F. Smith), (2) *Camponotus senex textor* Forel, (3) *Camponotus novogranadensis* Mayr, (4) *Crematogaster* spp., (5) all other ants, and (6) no ants. Several species of *Crematogaster* are found within the study sites including *C. carinata* Mayr, *C. crinosa* Mayr, *C. formosa* Mayr,

*C. nigropilosa* Mayr, and *C. sumichrasti* Mayr. Unfortunately, these were not distinguished at the time field surveys were conducted and thus are treated as a genus here. Other common arboreal ants found in the study sites include *Pheidole* spp., *Nesomyrmex* spp., *Brachymyrmex* spp., and *Pseudomyrmex* spp. A total of 81 species of ants have been sampled from coffee plants and shade trees in the study sites from 1999–2003. Extensive information about ant diversity and abundance in the same sites is summarized in Philpott et al. (2006). I included only *A. instabilis*, *C. senex textor*, *C. novogranadensis*, and *Crematogaster* spp. as numerical dominants based on the fact that they were frequently encountered in the shade trees in the study sites.

I used ANOVA and Tukey's tests to verify differences in management intensity between all sites. For individual vegetation characteristics, I used a Bonferroni correction for multiple tests ( $\alpha=0.0125$ ); multivariate statistics were unpractical because not all variables were measured on all dates. Tree circumference and SUN were only sampled once and were not included in statistical comparisons. To test for relationships between the management index and ant occurrence on coffee plants or shade trees, I used multiple regressions. Because plots sampled on different dates do not constitute independent data points, I averaged management index values and ant occurrence frequency (proportion of total coffee plants or shade trees with ants) for use in regressions. I first tested for relationships between occurrence frequency on coffee plants and shade trees and the management index for all species, numerical dominants, and other ants combined. I then tested data for each species separately.

#### Quantifying ant patchiness in the coffee layer and around shade trees

To quantitatively test for ant patchiness within species, I developed two models, conceptually equivalent to two-tailed *t* tests, using Pascal (Turbo 5). With each model, I compared data for observed ant spatial distribution patterns (field data) to computer-generated, randomized spatial distribution patterns. Each model thus simultaneously evaluated if ants formed single-species patches or were distributed at random or in uniform patterns. The two models differed in that model I examined patchiness in the coffee layer (excluding the shade trees) and model II examined patchiness relative to the shade trees. Model II specifically tested the prediction that shade tree location determines patch placement within coffee agroecosystems. Models I and II separately analyzed data from each date and plot and for each numerically dominant species. For observed (i.e., field collected) data, the models counted the number of coffee neighbors that contained conspecifics relative to other coffee plants (model I) or shade trees (model II). The numbers of coffee neighbors with conspecifics were summed across all coffee plants or shade trees in a given plot for each species. The models repeated this process 1,000 times for computer-generated data sets

where the model randomly assigned coffee plants to an ant category with the same frequency in which they were observed in the field. The model then compared observed data to the frequency distributions created to determine if each species was more likely than random to occur on neighbors (patchy), less likely to occur (uniform), or equally as likely to occur (randomly distributed). The outcome from the two models indicated for each plot and sampling date if each species was distributed in patches, at random, or uniformly in the coffee plant layer (model I) or in coffee plants around shade trees with the same ant species (model II). During each run of the model, every coffee plant (I) or shade tree (II) in the plot was used as a focal point around which neighbors were assessed. For each plot and date, I ran models four times using distinct neighbor distances (3, 5, and 10 m or the ten closest plants) to determine which scale, if any, best captured ant patchiness for each species. At times during field surveys, I found more than one numerical dominant species on a coffee plant or shade tree. However, because running models was highly time intensive (20 min per simulation for >300 simulations), I assigned plants to one species giving priority to *A. instabilis*, then *C. senex textor*, then *Crematogaster* spp., ultimately limiting the number of additional simulations needed. In some plots, one or more species were absent or infrequently encountered, thus models were programmed to run if an ant species was found on more than two plants per plot.

To determine overall patterns of species-specific patchiness and changes due to distance, strata, or management intensity, I compiled data for each plot across all dates. It was not surprising that ant distribution patterns did differ somewhat among dates for particular plots, but I was more interested in comparing plots under different management systems. For each plot, I counted on how many dates each species was distributed in patches, uniformly, or at random and converted these frequencies into percent of total observations for a total of nine data points per species. Overall patterns of patchiness for all plots, ants, distances, and strata (coffee and shade trees) were assessed qualitatively. To test if patchiness varied with distance or depending on whether the focal tree was a coffee plant or shade tree, I used MANOVA using the percent of trials that were patchy for each species as the dependent variables and distance (3, 5, and 10 m or the nearest ten plants) and strata (coffee or shade tree) as main factors. I also tested if patchiness varied with coffee management intensity. I used multiple regressions to examine if the percent of trials in which ants were patchy correlated with the management index. I used one test for each numerical dominant where percent of trials that were patchy at each distance and strata were treated as the dependent variables (eight in each regression) and management intensity as the independent variable.

## Results

### Effects of management intensity on ant occurrence

Management intensity differed significantly between sites as measured in terms of individual vegetation variables and the management index (Table 1). For all species, numerical dominants, and other ants combined, occurrence frequency was significantly correlated with increasing management intensity ( $R^2=0.715$ ;  $F=17.587$ ;  $df=1,7$ ;  $P=0.004$ ). With increasing intensity, occurrence frequency of one numerical dominant, but not of others, significantly declined (Fig. 1). On both coffee plants and shade trees, occurrence of *A. instabilis* declined with increasing intensity ( $R^2=0.485$ ;  $F=6.59$ ;  $df=1,7$ ;  $P=0.037$ ). The occurrence of other (not numerically dominant) ants increased with management intensification ( $R^2=0.448$ ;  $F=5.68$ ;  $df=1,7$ ;  $P=0.048$ ). Individual occurrence of *C. senex textor*, *C. novogranadensis* and *Crematogaster* spp. did not vary with management intensity.

### Effects of distance and strata on ant patchiness

All numerically dominant ant species sampled formed patches in the coffee layer and shade in at least some trials, but the proportion of trials in which ants were patchy differed by species identity, distance, and strata (Fig. 2). For all distances, *A. instabilis* was patchy in both the coffee layer (65–96% of trials) and around the shade trees (73–83% of trials). In roughly half of trials in the coffee layer, *C. senex textor* formed patches (48–59%), and this ant was patchy less often in the shade trees (21–47%). The proportion of trials in which *C. novogranadensis* was

patchy ranged greatly with distance in the coffee layer (30–84%) as well as around shade trees (40–88%). Finally, *Crematogaster* spp. were patchy in 37–76% of trials in the coffee layer and in 25–40% of trials with shade trees. Overall, ant patchiness, however, did not differ consistently with distance from focal trees or with strata (Table 2). Nonetheless, between-subjects tests on a per-species basis showed that the percent of trials in which *Crematogaster* spp. were patchy was significantly higher for the coffee layer. Furthermore, *C. novogranadensis* was more likely to be patchy at the distance of 3 m than that at 10 m (Tukey's test,  $P=0.024$ ), but the percent of trials where this ant was patchy did not differ for other distances.

### Ant patchiness and management intensity

In general, the percent of trials in which ants were patchy did not correlate with changes in coffee management intensity. For none of the distances or strata included did any numerically dominant ant patchiness correlate with changes in management intensity: *A. instabilis* ( $R^2=0.018$ ,  $F=0.0768$ ,  $df=1, 4$ ,  $P=0.7953$ ), *C. senex textor* ( $R^2=0.2518$ ,  $F=1.346$ ,  $df=1, 4$ ,  $P=0.3104$ ), *C. novogranadensis* ( $R^2=0.006$ ,  $F=0.027$ ,  $df=1, 4$ ,  $P=0.8779$ ), and *Crematogaster* spp. ( $R^2=0.039$ ,  $F=0.163$ ,  $df=1, 4$ ,  $P=0.706$ ). Because multivariate tests did not show significant overall patterns, no tests for individual strata or distances were conducted.

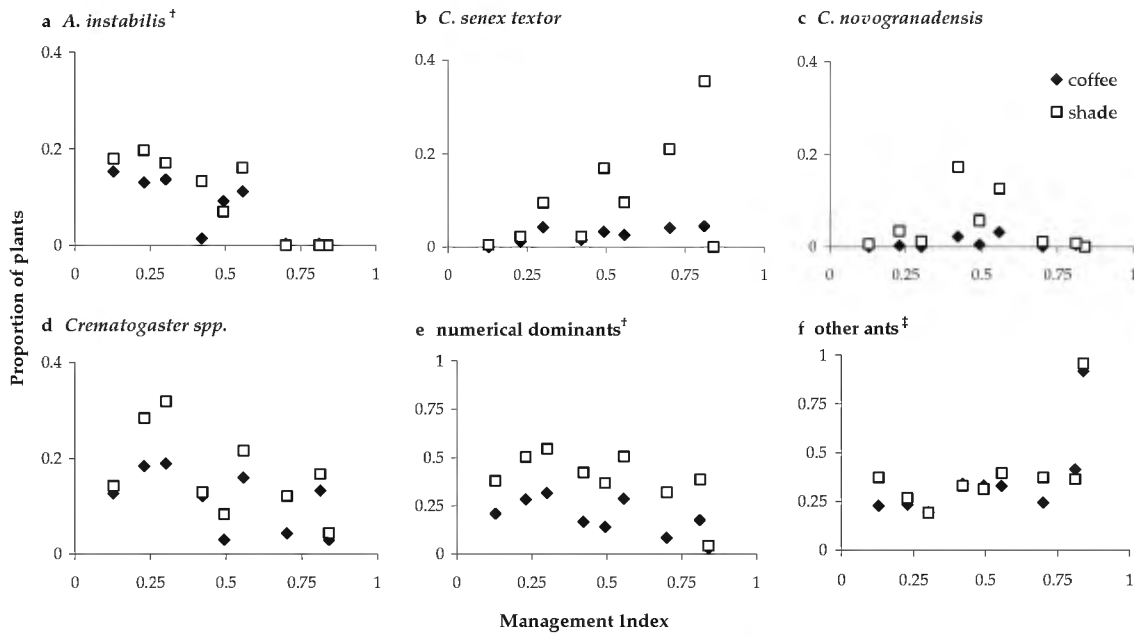
## Discussion

The proportion of coffee and shade trees with numerically dominant ants overall declined with coffee management

**Table 1** Site vegetation characteristics and management index (MI) for coffee sites as selected to represent a gradient of management intensification

Sites	Vegetation variables		Percent cover (%)	Trees >100 cm	No. of tree morphospecies	Management index (MI)	No. of times sampled
	No. of coffee plants	No. of shade trees					
TPB2	96.00±0.58 (a)	51.75±1.11 (a)	95.50±1.71 (a)	9.00	17.50±0.20 (a)	0.13±0.02 (a)	4
TPB1	140.20±0.49 (ab)	36.40±0.24 (b)	91.60±0.75 (ab)	16.00	11.50±0.47 (b)	0.23±0.02 (ab)	5
TPI	201.40±14.35 (bc)	37.00±2.12 (b)	94.00±1.79 (ab)	11.00	9.50±0.16 (bc)	0.30±0.02 (bc)	5
CPB1	306.60±5.10 (cd)	36.60±0.51 (b)	74.80±4.32 (ab)	6.00	11.00±0.32 (b)	0.42±0.02 (cd)	5
CPI	278.60±12.95 (d)	26.80±0.97 (bc)	78.40±1.33 (ab)	3.00	6.50±0.16 (cd)	0.49±0.02 (d)	5
CPB2	331.25±2.06 (de)	21.25±4.17 (cd)	53.00±4.79 (c)	8.00	9.50±0.20 (bc)	0.56±0.03 (de)	4
SM2	470.00±13.46 (e)	16.20±0.66 (cd)	70.40±6.11 (bc)	2.00	4.50±0.16 (d)	0.70±0.04 (e)	5
SM1	494.00±28.12 (ef)	14.40±4.97 (d)	24.00±7.09 (d)	2.00	8.50±0.16 (cd)	0.81±0.07 (f)	5
SUN	441.00 (na)	10.00 (na)	12.00 (na)	0.00	6.00 (na)	0.84 (na)	1
<i>P</i>	<0.001	<0.001	<0.001	na	<0.001	<0.001	
<i>F</i>	95.7	25.9	27.1	na	25.1	41.867	
<i>df</i>	1,7	1,7	1,7	na	1,7	1,7	

Sites are arranged in order of increasing management intensity from traditional polycultures (TPB2, TPB1, and TPI), commercial polycultures (CPB1, CPI, and CPB2), shade monocultures (SM2 and SM1) to unshaded sun coffee (SUN) and were distributed in four farms in the Soconusco region of Chiapas (Belen, Irlanda, Hamburgo, and Guadalupe Zajú). Numbers are mean values (±SE) across a total of 1–5 sampling dates for each plot. Statistical results are for univariate ANOVA and different letters in parentheses represent plots for which vegetation variables ( $\alpha=0.0125$ ) and MI ( $\alpha=0.05$ ) significantly differed. Higher MI values indicate higher management intensity. The SUN site and tree circumference were only sampled once and are not included in statistical comparisons (na)



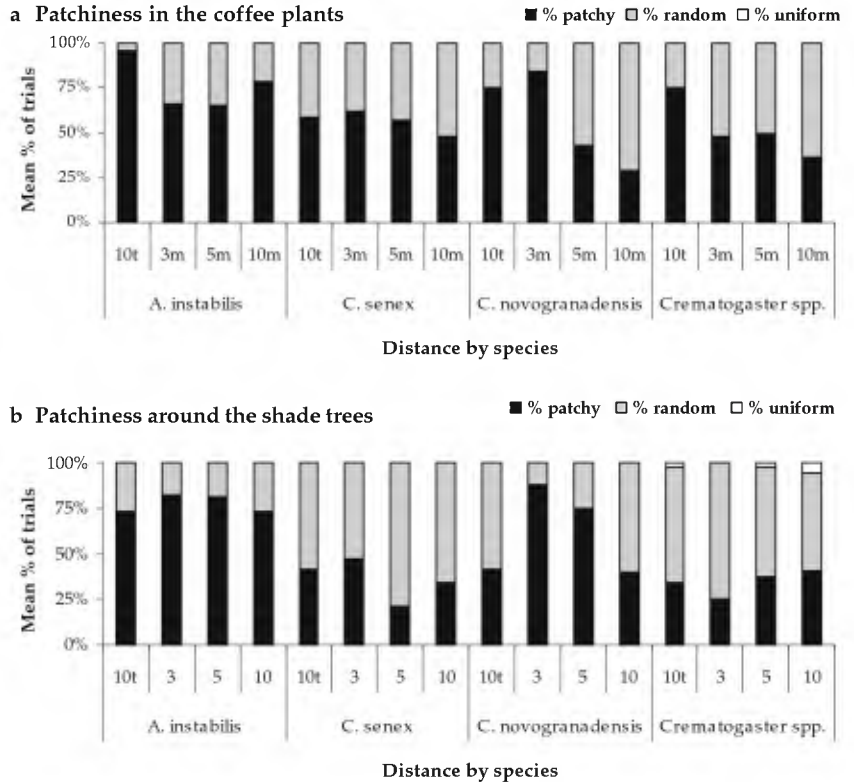
**Fig. 1** Occurrence frequency of numerical dominants and other ants as a function of management intensity. Symbols show proportion of coffee plants (closed diamonds) and shade trees (open squares) with **a** *A. instabilis*, **b** *C. senex textor*, **c** *C. novogranadensis*, **d** *Crematogaster* spp., **e** all numerical dominant ants, and **f** other non-numerical dominants. The management index measured coffee

management intensity (Table 1), and high values correspond to more intensive management. Dagger (†) indicates that occurrence decreased significantly with management index and double dagger (‡) indicates that occurrence increased significantly with management index (see text for details)

intensification, but this pattern was entirely driven by declines of *A. instabilis*; the other numerically dominant species were not affected by intensification. All ant species formed statistically distinguishable single-taxon patches in

at least some plots on some sample dates. Although the analyses carried out here do not allow detailed quantitative comparisons between species, the patterns observed suggest that *A. instabilis* was patchy in a higher proportion

**Fig. 2** Numerical dominant ant patchiness in coffee agroeco-systems as a factor of strata, distance, and species. Bars show mean percents of model trials and for which distances [3, 5, and 10 m, or the ten closest trees (10t)] for ant taxa (see Fig. 1) were distributed in patches, at random, or uniformly in the coffee plant layer (a) or around shade trees (b) in 25×50-m-plots species



**Table 2** Ant patchiness as a factor of ant identity, distance or size of patches, and strata

MANOVA		df	F	P
	Distance	4, 24	2.247	0.094
	Strata	4, 22	1.897	0.147
	Distance × strata	4, 24	1.249	0.317
Between-subjects effects				
Distance	<i>A. instabilis</i>	3, 25	0.138	0.937
	<i>C. senex textor</i>	3, 25	1.16	0.344
	<i>C. novogranadensis</i>	3, 25	2.67	0.069
	<i>Crematogaster</i> spp.	3, 25	0.674	0.576
Strata	<i>A. instabilis</i>	1, 25	0.047	0.831
	<i>C. senex textor</i>	1, 25	0.476	0.497
	<i>C. novogranadensis</i>	1, 25	0.026	0.872
	<i>Crematogaster</i> spp.	1, 25	8.536	<b>0.007</b>
Distance × strata	<i>A. instabilis</i>	3, 25	1.452	0.251
	<i>C. senex textor</i>	3, 25	0.166	0.918
	<i>C. novogranadensis</i>	3, 25	0.931	0.44
	<i>Crematogaster</i> spp.	3, 25	0.281	0.839

Results show MANOVA using percent of trials in which each ant species was distributed in patches as the dependent variable and distance (3, 5, and 10 m or the ten closest trees) and strata (within the coffee layer or around shade trees) as main factors. *Bold print* shows significant ( $P < 0.05$ ) factors

of trials both in the coffee layer and around shade trees than the other species were. Only *A. instabilis* appeared to consistently form patches around shade trees. *C. senex textor* was patchy in approximately half or a little fewer than half of trials. Patterns for *C. novogranadensis* showed much wider variation in the percent of trials where this ant was patchy than did other species. Statistical tests indicated that *C. novogranadensis* were significantly more patchy at shorter distances, such that they formed patches in a lower percentage of trials at 10 m than at 3 m. Finally, *Crematogaster* spp. were relatively rarely patchy compared to other species, especially around shade trees. *Crematogaster* spp. formed patches less frequently around shade trees than in the coffee layer. Patchiness of none of the ants, however, was affected by coffee management intensity, indicating that this anthropogenic disturbance may not influence formation of single-species patches.

Patchiness greatly varied between species, as *A. instabilis* was always patchy whereas other ant species were only patchy at some distances or only in the coffee plants and not in coffee plants around the shade trees. *A. instabilis* formed tight patches up to 10 m from coffee and shade trees in all management systems, even though *A. instabilis* abundance declined with intensification. The two patterns showing that *A. instabilis* occurrence declined with management intensification and that this species very frequently formed patches around shade trees may indicate that trees are a very important resource for this species and may in part determine its spatial distribution (i.e., patch location) within coffee agroecosystems but not patch formation. In particular, *A. instabilis* tend to nest in large trees within coffee farms (personal observation). Thus, intensifying production by removing shade trees would limit the number of plants per plot with this ant. *C. senex textor* is a nest-weaver (Forel 1899) and is more often

seen nesting in the coffee plants (personal observation). *Crematogaster* spp. and *C. novogranadensis* nest opportunistically in cavities and dead and live branches (Longino 2002) and, thus, may be ubiquitous in all parts of the coffee farms and not restricted to shade trees. Because ants were sampled differently in the coffee plants and shade trees, caution must be used in interpreting the results, as methodological differences may have influenced the apparent results. Due also to the fact that *Crematogaster* spp. were treated here as a genus and not as single species as is the characteristic of studies of ant spatial distributions, all results involving *Crematogaster* must be treated with caution. Different species of *Crematogaster* may have different nesting habits or food requirements, which may make examining their spatial distributions as a genus flawed.

Understanding and quantifying which factors determine ant spatial structure is critical to understand ant impacts on arthropod communities. According to this study, patchy patterns in ant communities are not influenced by changes in management intensity or, aside from *A. instabilis*, by shade tree locations. This is true despite the fact that fewer food and nesting resources are available in intensively managed coffee plantations (Moguel and Toledo 1999; Armbrrecht et al. 2004). In coffee plantations, most dominant ant species nest in the shade trees, although occasionally *A. instabilis*, *C. senex textor*, or *Crematogaster* spp. nests are found in the coffee bushes (personal observation). Thus, removal of shade trees would be expected to limit one important resource for dominant ants—nest sites. Furthermore, resources such as extrafloral nectar found on shade trees (such as *Inga* spp.) are important diet components of these ants (Davidson et al. 2003) as are homopterans and other arboreal arthropods. In the study sites, arboreal ant diversity declines with

intensification (Philpott et al. 2006) and some have suggested that, where diversity is higher, it is unnecessary or difficult for one ant species to dominate a particular area or patch (Hölldobler and Wilson 1990). Furthermore, patchy distributions of ants are not found in many natural forests because of lower resource availability (e.g., Floren and Linsenmair 2000). My results, however, provide little evidence that management intensification within this particular gradient, lower ant diversity, or a lower supply of available resources relate to changes in ant spatial patterns.

Many alternative hypotheses – including many that have already been examined qualitatively – could be tested with the same types of spatially explicit quantitative techniques presented here. Nest site specialization or niche partitioning could be examined to test if ant distributions follow closely particular tree species (Djieto-Lordon and Dejean 1999). Ant distribution patterns have elucidated that particular dominant ants associate with homopterans or other arthropods (Leston 1973; Majer 1978; Majer et al. 1994; Dejean et al. 1997). Different resource preferences among ant species may also structure ant communities in patches. This same model could be used to examine relationships between ant patterns and such resources. Furthermore, such a model could be used to examine other types of physical or temporal habitat specialization among ant species or examine aspects of interspecific competition such as negative relationships among ant species.

In summary, most ant species were patchily distributed in at least some trials at some scales, upholding a quantitative test of single-species ant patchiness across a coffee landscape. Of all species examined, *A. instabilis* appeared to be the most often patchy and this patchiness was associated with shade trees. The model used here was useful to determine if ant patchiness differs with scale and management intensity and could also shed light on alternative hypotheses to explain patchy distributions of ants.

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