Limitation of nesting resources for ants in Colombian forests and coffee plantations

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Abstract. 1. This study examines limitation of nesting resources for leaf-litter and twig-nesting ants as a mechanism of diversity loss across an intensification gradient of coffee production in Colombia. Twelve farms were selected and classified into four management types: forest, polygeneric shade coffee, monogeneric shade coffee, and sun coffee (unshaded coffee monocultures).

2. At each of the farms, four treatment subplots were established at the corners of each of 10 25 m^2 plots: (i) twig augmentation (adding 10 empty bamboo twigs); (ii) litter augmentation (tripling existing litter profile); (iii) twig and litter augmentation; and (iv) no manipulation control, for a total of 480 subplots. A twig addition experiment was also performed on coffee bushes.

3. The results showed significantly more ant colonies in the forest and monogeneric shade coffee litter augmentation plots after 4 months. Litter-nesting ant species richness was higher in all three shade systems than in the sun coffee. The identities of ants nesting on coffee bushes were different from those in the soil level litter. Fewer species nested in bamboo twigs placed in litter in the most intensive systems.

4. More ants nested in the resource addition treatments, and more ant species were found in forested habitats; however, a single mechanism cannot explain the observed patterns. It was concluded that a combination of bottom-up and top-down effects might lead to the loss of associated fauna with the intensification of these agroecosystems.

Key words. Biodiversity loss, Formicidae, leaf-litter ants, resource limitation, twig-nesting ants.

Introduction

Coffee production systems fall into different intensity classes, representing gradients of intensification in which forest-like traditional coffee is the most biologically diverse. Such traditional shade systems, however, are increasingly transformed into coffee farms with little shade and high agrochemical inputs. This is associated with reduced biodiversity of arthropods, birds, and other vertebrates (Borrero, 1986; Gallina *et al.*, 1992; Perfecto & Snelling, 1995; Perfecto *et al.*, 1996; Greenberg *et al.*, 1997; Moguel & Toledo, 1999). Here, the effect of agricultural intensification on ant communities is examined. Ants constitute an ecologically sensitive group for indicative changes in biodiver-

sity (Kaspari, 1996b; Baur *et al.*, 1998; Agosti *et al.*, 2000; Perfecto & Vandermeer, 2002) because of their ubiquity and abundance (Majer *et al.*, 1997; Ward, 2000).

The loss of shade trees may produce a shortage of nesting sites and resources, such as twigs, logs, roots, seeds, leaf-litter, and bark, leading to reduced ant biodiversity. Lack of nesting sites has been suggested to cause loss of ant biodiversity along the agricultural intensification gradient (Perfecto & Vandermeer, 1996; Armbrecht & Perfecto, 2003; Armbrecht *et al.*, 2004; Philpott & Foster, 2005). The extent to which nesting site availability limits ants in the agroecological context, however, is not known. Torres (1984) in Puerto Rico found little evidence that nest resources limited ground dwelling ants. By contrast, Kaspari (1996a) using twig augmentation experiments found partial evidence of nest site limitation in forests in Panama and Costa Rica and suggested that litter ant distributions may form a 'fluid mosaic', tracking the shifting availability of nest sites. On the other hand, he also argued

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that resource competition may not be the dominant factor regulating the distribution of leaf-litter ant species (*sensu* Levings & Traniello, 1981; Levings & Franks, 1982) with mortality among reproductive colonies being high and density independent (Kaspari, 1996b). He suggested that patch dynamics are a better mechanism to describe leaf-litter ants distribution and abundance because (i) army ants and soil nesting ants prey on litter ants and maintain populations well below their carrying capacity, and (ii) flooding and small-scale catastrophes open up patches for rapid colonisation. Thus top-down processes (predation) may be structuring the litter ant community while bottom-up processes (competition, resource availability) may be controlling the much larger soil nesting species in tropical forests (Kaspari, 1996b).

The intensification of coffee production may result in a reduction of nesting resources for leaf litter ants. A preliminary study in Mexico (Armbrecht & Perfecto, 2003) found that ant colonies in twigs decreased significantly with distance from the forest in a monogeneric shade coffee plantation, but not in a neighbouring polygeneric shade coffee plantation. Arboreal ants are not strongly nest-limited in the shaded coffee agroecosystems in Mexico, but nest-limitation increases with increasing management intensification (Philpott & Foster, 2005). If ants are indeed limited by nest resources, re-establishing tree cover or providing artificial nesting resources (e.g. hollow bamboo twigs) could increase ant diversity and density increasing the potential benefit of ants as predators (Perfecto & Castiñeiras, 1998).

The mechanism accounting for the changing communities of twig-nesting ants between vertical strata across an intensification gradient of coffee production remains unknown. In the Neotropics, *Pheidole* and *Solenopsis* are the numerically dominant genera of litter and soil dwelling ants (Byrne, 1994; Kaspari, 1996b; Delabie *et al.*, 2000; Perfecto & Vandermeer, 2002; Ramos-Suárez *et al.*, 2002; Franco *et al.*, 2003). This study asks whether litter and coffee twig-nesting species are limited by nesting resources under different shade management regimes. It was hypothesised that limitation via reduced nesting resources will increase with the intensification of coffee production and predict a stronger response to resource addition under the most intensive management regimes.

Methods

Study site

This study was conducted at farms in the Apía Municipality, Colombia (5°08′N; 75°56′W), at elevations between 1400 and 1900 m a.s.l., with a mean annual temperature of 20 °C and seasonal annual precipitation totalling 2320 mm. The region comprises secondary forest fragments scattered within an agricultural landscape, with forests becoming continuous at higher altitudes.

Four systems, forest, organic polygeneric shade coffee, monogeneric shade coffee, and sun coffee (coffee monocultures without shade trees) (Armbrecht *et al.*, 2005) were used each with three replicates (Table 1). Forests were isolated patches of disturbed secondary forest with dense, natural vegetation and closed canopies approximately 15 m high. Polygeneric shade coffee farms had a moderate diversity of shade trees, patchily scattered throughout (Armbrecht, 2003). These farms were organic with no pesticides or chemical fertilisers used for at least the past 4 years. Monogeneric farms (Nestel & Altieri, 1992) had a single dominant tree genus, but this differed among farms (*Cordia alliodora* [R. et P.] Cham. in MS1 and *Inga edulis* Mart in MS2 and MS3). The polygeneric shade farms were less intensive than monogeneric farms in that they were under organic management, had more species of trees (> 10 spp. ha⁻¹) and provided more shade (65%) compared with monogeneric shade farms (53%). Sun coffee plantations included scattered plantains and occasionally an isolated tree. In Sun1 and Sun2, the shade trees had been removed 2 years previous to the study, but 12 years earlier in Sun3.

The degree of management intervention in each farm was classified on a scale of 0–5 following Mas and Dietsch (2003) and described in Armbrecht (2003).

Litter-nesting experiments

In September 2001, 10 25 m² blocks, separated by 10 m from each other, were haphazardly established in each farm. Four 0.25 m² subplots were laid out at each corner of each block. Subplots were randomly assigned to one of four treatments:

Table 1. Description of 12 farms studied in the Apía municipality, Colombia.

Farm code	Management type	Farm's name	Area (ha)	Elevation (m a.s.l)
For1	Forest	Monteverde	15	1845
For2	Forest	Playabonita	2	1444
For3	Forest	El Porvenir	1.5	1.605
PS1	Polygeneric shade	La Playita I	15	1490
PS2	Polygeneric shade	La Playita II	19	1495
PS3	Polygeneric shade	La Clarita	7.5	1550
MS1	Monogeneric shade	Monteverde	4	1720
MS2	Monogeneric shade	Buenos Aires	6	1440
MS3	Monogeneric shade	Convenio	4	1465
Sun1	Unshaded	La Felisa	6	1480
Sun2	Unshaded	La Estrella	14	1470
Sun3	Unshaded	La Maria	3	1405

(1) 'control' with no manipulation; (2) 'litter augmented', litter depth increased × 3; (3) 'twig augmented', 10 hollow bamboo twigs added; and (4) 'twig and litter' augmented, treatments 2 and 3 combined. Bamboo twigs were 20 cm long and had external diameters of 2–4 cm. Response variables measured were the number of ant colonies in any of the substrates and the number of ant morphospecies per subplot. In total there were 120 blocks and 480 subplots. Subplots were protected from disturbance by a plastic mesh covering (1 cm^2 openings) fixed to the soil with 15 cm nails. Because the mesh was placed on top of all treatments, its presence should not have affected the addition subplots differently than the control subplots. Effects such as prevention of predation by birds or other vertebrates, however, were probably excluded by the mesh felt in all the treatments. Measurements were made 4 months after the initiation of the treatments in January 2002 (Byrne, 1994; Kaspari, 1996a). Ant colonies found inside the twigs or in the leaf litter were transported to the laboratory and samples from each were initially identified to genus and morphospecies (Holldobler & Wilson, 1990; Bolton, 1994; Fernández, 2003) before being later identified to species level by specialist taxonomists.

Canopy cover was measured with a spherical densiometer (Forestry Suppliers®, Jackson, MS) at the centre of each block. Litter depth (cm) was measured by gently forcing a ruler down to the upper soil layer at three haphazard points. All twigs less than 2.5 cm diameter in each subplot were counted.

Coffee bush twig-nesting experiment

A second experiment was conducted to test whether offering twig-nesting resources to ants on coffee bushes (1–1.5 m from the ground) would increase the number of ant colonies in bushes. In January 2002, 10 empty bamboo twigs were hung horizontally at approximately 1 m from the ground on the coffee bushes immediately above the two soil subplots, which were formerly twig augmented. The two coffee bushes above the soil subplots that received no twig augmentation were used as controls. This sums a total of 480 experimental units or coffee bushes (two treatments × two replicates within blocks × 10 blocks × 12 farms). After 4 months (May 2002) each bamboo augmented coffee bush was examined for number of ant colonies by both introducing a wire through each of the 10 bamboo twig holes and breaking all natural dry twigs from the coffee bush; each control coffee bush was checked for ant colonies by breaking all natural dry twigs from the bush. As there were very few coffee plants in the forest, other understory plants between 2 and 4 m height were used for the experiment.

Statistical analysis

A log-linear model with a Poisson error term was used to test the effects of management type, farm, and treatment on two response variables: the number of ant nests and the number of ant species. Farms were nested within management types and plots within farms. Both farms and plots were treated as random factors. Twig count (number of twigs in each subplot), litter depth,

and canopy cover were entered into the model as covariates. A Poisson model is appropriate in this case because the response variables represent counts of relatively infrequent events. Residual diagnostics suggested that the Poisson error term was more appropriate than an assumption of normality. Moreover, tests for overdispersion suggested that the Poisson model fit as well as the Negative Binomial model. The regression model was fit using STATA 6.0 for Windows (StataCorp, 2001; for details see Long, 1997; Cameron & Trivedi, 1998). A backwards selection method was then used to identify the best fit model for both response variables.

Statistical analyses involving the frequency distribution of ants nesting in bamboo twigs across the farms were performed using chi-square tests (Zar, 1999). The Kruskal–Wallis nonparametric test was used to compare more than two data sets when normality assumptions or homogeneity of variances were not met. Simple linear regression was used to relate nesting variables with canopy cover and intensification gradient.

The accumulated number of ant species nesting in each subplot was plotted by management type using Colwell's 5.1 EstimateS program (Colwell, 1997). Jacknife2 non-parametric estimator was used to estimate species richness because nonparametric estimators are appropriate for diverse taxa such as insects (McKamey, 1999).

Results

A total of 1466 ant colonies and 83 ant morphospecies were recorded, of which 778 colonies and 61 ant species were found in the litter-nesting experiment and 688 colonies and 38 species were recorded in the coffee bush experiment. Only 16 of the 83 species (19%) were found nesting in both litter and coffee bushes; 22 species (representing 58% of the coffee nesters) nested exclusively in coffee bushes, and 45 species (74% of the litter nesters) nested exclusively in litter. The distribution of ant species in vertical strata (i.e. soil, coffee bushes, both) was not uniform ($\chi^2_2 = 12.81$; $P = 0.02$).

The management index for each farm exhibited an increasing trend along the gradient of intensification from forests, polygeneric shade, monogeneric shade to sun with average management indices of 0.7, 2.3, 2.8 and 4.3 respectively.

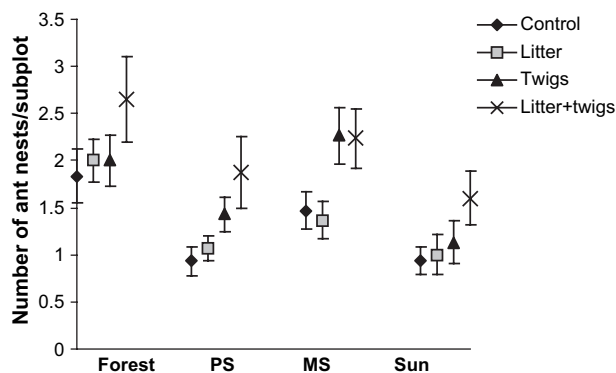### Litter-nesting experiment

The final Poisson regression model was highly significant for the number of ant colonies ($\chi^2_{18} = 90.05$, $P < 0.001$) (Table 2). This model identified two levels of management – forest and monogeneric shade – and two levels of treatment – twig augmentation and twig litter^{-1} augmentation – that resulted in significantly more colonies (Fig. 1 Table 3). Forest ($P < 0.001$) and monogeneric shade ($P < 0.001$) had 57.2% and 83.9% more nests respectively, than polygeneric shade and sun coffee systems (Tables 2 and 3). Twig addition (P = 0.009) and the twig and litter addition ($P < 0.001$) increased the number of nests per plot by 32.3% and 63.2% respectively, when contrasted with the no addition control and the litter only treatment.

Table 2. Microhabitat (columns 2–4) and response (columns 5–6) variables for the litter-nesting experiment (average $\pm$ standard error). Twig count (Kruskal–Wallis $\chi^2_3 = 96.27$; $P < 0.0001$), litter depth ($\chi^2_3 = 53.64$; $P < 0.0001$) and canopy cover ($\chi^2_3 = 357.46$; $P < 0.0001$) differed by management type.

Farm code	Canopy cover (%) $n = 10$	Litter depth (cm) $n = 40$	Twig count (no./subplot) $n = 40$	Colonies (no./subplot) $n = 40$	Ant species (no./subplot) $n = 40$
For1	82.7 ± 2.0	2.9 ± 0.2	9.8 ± 0.7	1.5 ± 0.16	1.3 ± 0.14
For2	90.9 ± 1.13	1.4 ± 0.2	8.2 ± 0.5	2.4 ± 0.34	1.6 ± 0.17
For3	88.5 ± 1.53	3.2 ± 0.2	10.0 ± 0.5	2.5 ± 0.21	1.9 ± 0.17
PS1	63.8 ± 3.9	2.7 ± 0.2	4.8 ± 0.5	1.5 ± 0.24	1.2 ± 0.12
PS2	59.5 ± 4.4	2.5 ± 0.2	4.6 ± 0.4	1.4 ± 0.22	1.0 ± 0.11
PS3	71.7 ± 2.6	5.2 ± 0.3	5.3 ± 0.5	1.1 ± 0.16	1.0 ± 0.11
MS1	32.3 ± 3.3	3.8 ± 0.3	6.1 ± 0.3	1.7 ± 0.22	1.2 ± 0.13
MS2	54.1 ± 4.5	2.5 ± 0.2	6.3 ± 0.5	2.4 ± 0.27	1.9 ± 0.17
MS3	72.2 ± 2.9	3.5 ± 0.3	7.6 ± 0.6	1.4 ± 0.15	1.3 ± 0.12
Sun1	7.7 ± 1.5	2.9 ± 0.2	5.8 ± 0.4	1.2 ± 0.21	0.9 ± 0.13
Sun2	10.2 ± 1.7	1.5 ± 0.1	8.9 ± 0.7	1.7 ± 0.19	1.3 ± 0.12
Sun3	17.2 ± 2.5	1.8 ± 0.1	2.8 ± 0.3	0.6 ± 0.14	0.5 ± 0.09

The final model for number ant species, which identified forest and monogeneric shade management having significantly more ant species (Table 3), was also highly significant ($\chi^2_6 = 75.91$; $P < 0.001$, Fig. 2, Tables 2 and 3). No effect of augmentation of nesting resources was detected on the number of ant species nesting in the subplots. No interactions were significant for either response variable.

Observed ant species richnesses were 37, 30, 30, and 26 for forests, monogeneric shade, polygeneric shade, and sun respectively. The Jack-knife estimator (Jack-2) of species richness (Colwell, 1997) were similar for the shaded coffee systems and forest, but lower for sun coffee (Fig. 3). No stronger response of richness to resources addition under any of the management regimes was detected for the Jack-2 and Chao-1 estimators when calculated separately for each of the four treatments within each of the management systems. For this analysis the average Jack-2 for the four treatments was 32, 25, 29, and 25 ant species for forest, polygeneric shade, monogeneric shade, and sun respectively, while Chao-1 estimator was 28, 26, 25, and 23 ant species respectively.

For the litter-nesting experiment, the most important nesting substrate was natural twigs (318 colonies of 3206 examined twigs), followed by the augmented bamboo (188 of 2400 examined bamboo twigs), litter (142), soil (90), decomposing logs (35), and seeds (5). The number of ant species nesting only in the bamboo twigs (not counting ant colonies nesting in other substrates as in Figs 1 and 2) was significantly and negatively related to the decreasing management index, i.e. the more intensive the system, the lower the number of ant species that colonised the bamboo twigs ($R^2 = 0.36$; $F_{1,10} = 5.6$; $P = 0.04$, Fig. 4).

Coffee bushes twig-nesting experiment

From the 480 experimental coffee bushes, 2573 natural coffee twigs and 2356 bamboo twigs were examined. A total of 566 ant colonies were found, 372 inside bamboo twigs, 150 in coffee twigs, and 44 in 'hanging twigs' falling from shade trees or climbing

Fig. 1. Mean ($+$ SE) numbers of ant colonies per treatment subplot in each management type. Management types are ordered according to increasing intensification: forests, polygeneric shade, monogeneric shade, and suns.

Table 3. Results from the Poisson regression for the number of ant nests and number of ant species. The second column (b) gives the coefficients fitted by the model to explain the log of the response mean relative to sun and polygeneric shade management types, and treatments 1 and 2 (control and litter augmented). Column 5, e^b, gives the b coefficients to indicate the proportional increase above the baseline. For example, 1.57 indicates a 57% increase in the number of nests above sun/polygeneric shade. The observed standard deviation for the response variables after fitting the model was 1.48 for number of nests and 0.94 for number of species; $n = 480$.

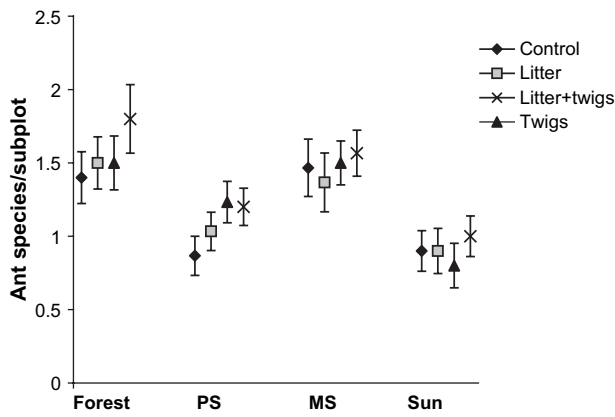| Treatment	b	Z	$P > |z|$	IRR (e^b)	%StdX
Number of nests					
Monogeneric	0.45	4.18	< 0.001	1.57	21.6
Forests	0.61	5.78	< 0.001	1.84	30.1
+Twigs	0.28	2.63	0.009	1.32	12.9
+Twigs and litter	0.49	4.80	< 0.001	1.63	23.7
Ant species					
Monogeneric	0.49	4.04	< 0.001	1.64	23.9
Forests	0.57	4.74	< 0.001	1.77	28.0

Fig. 2. Mean (+ SE) numbers of ant morphospecies nesting at each of the treatment subplots and management types. Management types are ordered according to increasing intensification.

Fig. 4. Plot of the relationship between the total number of ant species nesting in the leaf litter and the management index in each of 12 farms ($y = -1.12x + 7.54$, $R^2 = 0.36$).

weeds. The number of hanging twigs ($R^2 = 0.37$; $F_{1,10} = 5.77$; $P = 0.037$) and the number of colonies in hanging twigs ($R^2 = 0.47$; $F_{1,10} = 8.86$; $P = 0.014$) were positively related to the percentage of shade. The average number of coffee twigs opened in the search for ant colonies ranged from 2.4 to 7.2 dry twigs/coffee plant/farm. From 1946 dry coffee twigs opened, 5.3% were occupied by ant colonies in augmented treatments, while 4.0% (40 of 1009) were found in 'control' coffee bushes with no bamboo augmentation. *Procryptocerus scabriusculus* Forel represented more than half (53%) of all colonies found in coffee twigs. A significant correlation (Spearman's ρ = 0.51; $n = 19$; $P = 0.026$) was found between the number of colonies in coffee twigs and the number of twigs opened per coffee plant ('zero' values were discarded for the test). The percentage of ant colonies inside bamboo in the coffee bushes experiment in each farm was significant and positively related to the increasing intensification of the coffee farms ($R^2 = 0.56$; $F_{1,10} = 12.78$; $P = 0.005$). The number of species, however, did not show any trend across the gradient of intensification of coffee production (average 5.62; Pearson regression $P > 0.7$).

Paratrechina cf. *steinheili* was found to be the most abundant nesting ant in the study with 286 colonies (100 in coffee bushes
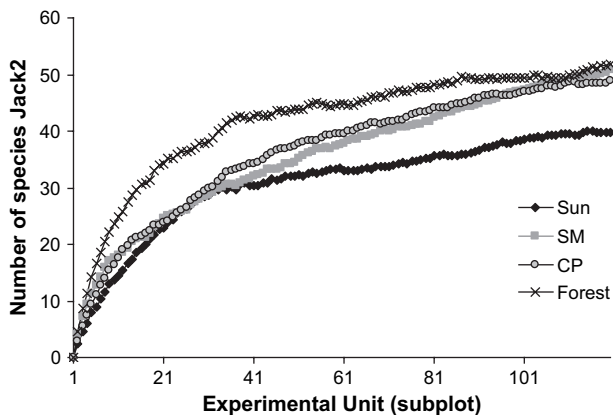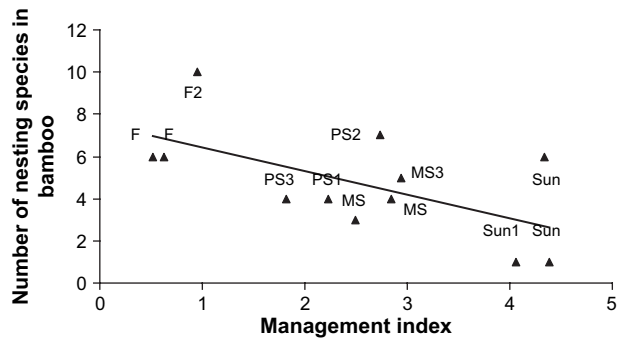

Fig. 3. Jack-knife2 estimated number of litter-nesting ant morphospecies (50 randomisations) for each management type.

and 186 in litter). In the litter experiment, this species was distributed as follows: 67 colonies in bamboo, 45 in natural twigs, 68 in leaf litter and six in other nesting substrates. This same ant species was the second most abundant nester in polygeneric shade farms (16.3%) but was not detected at all in Sun3, where its nesting resources had almost disappeared. The most abundant species nesting in leaf litter tended to represent a higher percentage of all colonies found as shade decreased. The composition of litter-nesting dominant ants was different in the forests, where some solitary hunting Ectatomminae and Ponerinae ants were important in litter: *Gnamptogenys bisulca* accounted for 39% of the colonies in Forest1, *Hypoponera* sp. 1 for 28% colonies in Forest2, and *Pheidole* cf. *ebenina* 34% (Myrmicinae) followed by *Hypoponera* sp. 2 with 12% of colonies in Forest3. For *P. steinheili*, the increase in the number of colonies in the augmentation treatment (number of colonies in twig and litter augmentation treatment/number of colonies in control plots) was positively related to the management index ($R^2 = 0.88$; $F_{1,8} = 29.91$; $P = 0.001$), i.e. the more intensified the farm, the higher relative abundance of this ant species compared with the control subplots.

An analysis of the two vertical strata (ground and coffee bushes levels), showed that an average of 66% colonies in coffee bushes belonged to 11 ant species, from which nine (82%) were never found nesting in litter. As for litter-nesting ants, 16 ant species accounted for 53% of all colonies, from which 13 (82%) species were never found nesting on the coffee bushes in any of the farms.

Discussion

The predictions derived from the initial hypothesis were only partially supported in this study. From the results of this study it cannot be stated that bottom-up mechanisms, such as the lack of nesting resources, are the only ones responsible for ant diversity loss when coffee agriculture is intensified. This consideration is supported by the fact that there was no significant interaction between management and litter treatment, which also suggests that the nest site litter limitation result is robust. Further, the positive response to the addition of nesting resources for ants occurred along the whole gradient of intensification and not only in the most intensive coffee plantations (Figs 1 and 2). Twig resources appear to be a limiting factor, but the effect on

the number of ant colonies was greater when accompanied by litter addition. The addition of litter probably buffered microclimate changes and enhanced twig colonisation (e.g. Perfecto & Vandermeer, 1996). Additionally, considering that litter provides both food and nest sites it might be expected that an addition of both resources will produce a stronger respond from litter-nesting ants. Twig augmentation alone significantly increased the number of ant colonies both in monogeneric and polygeneric shade farms (Fig. 1), there were no interactions, possibly because litter already present contributed to the effect of twig addition. This explanation is supported by a higher litter depth measurement in both systems (monogeneric shade farms and polygeneric shade farms average 3.3 cm and 3.5 cm respectively, vs. 2.5 cm and 2.1 cm in forests and sun coffee farms respectively, Table 2). None of the covariates explained changes in the number of colonies, however, and the response can be attributed only to the augmentation treatments. The effect was consistent across the management types.

Nesting limitation has also been reported for other Neotropical natural habitats. Kaspari (1996a) concluded that nesting-site resources may limit local patchiness of ant colonies in forests in Panama and Costa Rica, although the litter ant populations did not grow large enough to saturate the environment because of the unstable litter environment. At La Selva, Costa Rica, Byrne (1994) found ant colonies in 6.4% of the available natural twigs on the forest floor, while 14% of the augmented artificial twigs were colonised by ants after 2 months, which is consistent with the ranges of 1.5–13% occupancy in artificial twigs and 9.9% occupancy in natural twigs by ant colonies found in this study.

Grain and diversity

In this study the available nesting resources were quickly occupied by the litter ant community (i.e. augmented bamboo twigs, as in Byrne, 1994; Kaspari, 1996a) and more species were present in the shaded systems. Monogeneric shade farms had more colonies and a higher species density (0.25 m² scale) than in the organic polygeneric shade coffee farms. This result may be attributable in part to more natural twig counts in the former (average 6.7 and 4.9 in monogeneric shade and polygeneric shade respectively), and also because *Paratrechina* cf. *steinheili* quickly occupied the bamboo and litter augmented resources in the monogeneric shade. Nevertheless the richness at the farm-scale in monogeneric shade was similar to that in polygeneric shade. An independent study in the same farms (Armbrecht *et al.*, 2005) showed that there is a dramatic reduction of leaf litter ant diversity with intensification of coffee production and different ant guilds are affected in different ways (Armbrecht *et al.*, 2004; Rivera & Armbrecht, 2005). The average Jack-2 and Chao-1 estimators (four treatments) showing a higher ant richness in forests and shaded coffee systems over sun coffee confirm these results.

The lack of significant differences in the number of species between polygeneric shade and sun coffee plantations shows that, although twig and litter augmentation resulted in an increase in the number of ant colonies, it did not increase the species density at the 0.25 m² scale. Species density is not always a good predictor of the species richness in a given habitat (Gotelli & Colwell, 2001) and it was evident that polygeneric shaded coffee plantations preserved a high species richness of twig litter⁻¹ nesting ants at broader spatial scales (Fig. 3).

The explanation for finding as many ant species at the fine scale (subplot) in the polygeneric shade farms as in the sun farms (Fig. 2) may be due to a combination of factors. First, the transformation of shade coffee into sun coffee at higher elevations is less deleterious for thermophilic taxa than at low elevations, where similar studies had been conducted (Perfecto & Vandermeer, 1996; Ramos-Suarez *et al.*, 2002) allowing higher densities within them. This explanation could be the case for *Paratrechina* cf. *steinheili*, a leaf-litter nesting ant that had been shown to resist successfully wide thermal fluctuations in laboratory conditions (Vargas *et al.*, 2006). This species was not found at all in Sun3, however, which was the most intensively managed coffee plantation of the study.

A second explanation are top-down mechanisms in polygeneric shade farms exerted by predatory ants. Both, the arboreal *Myrmelachista* 'az' and the litter-dwelling *Pheidole biconstricta*, were observed predating on other ant species (or their brood) in the field. As this top-down mechanism is very likely to operate in forests as well, a similar effect in ant richness at a fine scale would be expected in the forests, which was not the case. Finally, a third (but not exclusive) explanation for lower species density at the fine scale in polygeneric shade may be related to the organic management, in which the type of compost used, called 'Super 4', includes coffee pulp residues. It is known that caffeine, the major methylxanthine found in tea and coffee (including berries), inhibits insect feeding and is pesticidal at concentrations known to occur in plants (Nathanson, 1984). The compost probably negatively affects only the certain areas just under the coffee bush (where the treatments were placed), but not all areas around the bush homogeneously. The compost may explain why the overall richness was so high in the polygeneric shade (Fig. 3) despite having relatively low species density at finer scale. This effect would not operate within the forests. The implications of the spatial scale for conservation are obvious: the larger the area under 'environmentally friendly' management (organic) the more protection for more (ant) species.

The highly significant negative relationship between the number of *P. steinheili* colonies and increasing intensification index of the farms leads to the hypothesis that bottom-up forces, such as nesting resources, limit *Paratrechina* cf. *steinheili* populations in highly intensive sun coffee (Sun3), where they may be free from competition or predation from other ant species and can respond very quickly to the addition of nesting resources. Top-down regulation processes may become important as system complexity increases in more shaded systems. Results from this study showed that fewer ant species were responsible for the greater number of ant colonies in augmented treatments in the most intensive coffee systems, while in the polygeneric shade coffee plantations, the limitation of nesting resources was due to a larger number of ant species responding at a larger spatial scale.

A different picture emerges when analysing ant assemblages in coffee bushes. Nesting limitation for twigs appears to be very

strong in coffee bushes in sun coffee systems. Although only 8% of the bamboo twigs were colonised in the most intensive farm, Sun3, 94.2% of all the coffee bush colonies in this plantation were in bamboo (for comparison: 61, 82, and 43% in monogeneric shade, polygeneric shade, and forests respectively). The fact that a highly significant trend in the proportion of bamboo colonies along the gradient did not translate into an equally important trend in the number of ant species nesting in bamboo implies that offering more nesting resources does not allow more species to establish in the sun coffee plantations as source populations probably come from the same habitat. Pools of ant species colonising bamboo could be more adapted to desiccation in sun coffee (Sun3). No evidence was found, however, that *Crematogaster* sp. and *Camponotus* sp., the two species most responsible for bamboo colonisation, can resist dehydration better than other species. A strong nest site limitation is supported by the significant relation between 'hanging twigs', which are nesting resources originating mostly from shade trees. Additionally, the adverse habitat conditions in sun coffee might deter any possible establishment of new species in the most intensive plantations. These results is consistent with the work of Philpott and Foster (2005) who found a decrease in the number of arboreal ant species colonising artificial bamboo twigs as coffee intensification increased in Chiapas, Mexico.

A vertical stratification was shown (yet biotic interactions do exist; Hahn & Wheeler, 2002) in terms of nesting ants identities at the 1 m scale, even in the same locations and the same nesting resources (bamboo). Identities of twig-nesting ants in coffee bushes were not consistent across the intensification gradient and were very different from that in the litter. This result raises questions about the consequences of removing the arboreal ant mosaic systems along with the shade trees (Majer *et al.*, 1994; Dejean *et al.*, 1999; Armbrecht *et al.*, 2001) and the possibility of providing artificial nesting sites to stimulate certain populations of beneficial (predator) ant species in coffee plantations.

This study demonstrates that twig-nesting ants are limited by nesting resources in both leaf litter and coffee bushes. For litter-nesting ants, more ant species were found with increasing shade and decreasing intensification of coffee production. For the ants nesting in coffee bushes, the limitation tends to be greater in unshaded coffee farms. The complexity of the farm system studied prevents the formulation of a single mechanism to explain biodiversity loss. Bottom-up forces, however, such as the shortage of nesting resources for coffee bush nesting ants and changes in microhabitat conditions for litter-nesting ants, may become increasingly important to explain the loss of diversity of litter ants when the traditional, forest-like coffee farms are transformed into intensive, unshaded, coffee plantations.

Acknowledgements

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