

Research article

Impact of tree isolation on arboreal and ground ant communities in cleared pasture in the Atlantic rain forest region of Bahia, Brazil

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Summary. The Atlantic rain forest of south-eastern Brazil has been substantially cleared, resulting in the creation of a fragmented landscape. In addition to the small fragments of forest that remain, the pasture is often scattered with isolated trees. This paper investigates the capacity of these isolated trees to support representatives of the original Atlantic rain forest ant communities and also how these arboreal ants interact with the disturbance-associated ant fauna of the pasture beneath them. Twenty trees in the grassland, representing a range of distances from the forest, and 10 trees within the forest, were selected for sampling. Arboreal ants were sampled by hand collection and chemical knockdown, while the ants on the ground beneath were sampled by pitfall traps and Winkler sacks. Pasture trees supported a moderately high richness of arboreal ant species. The richness of ants on pasture trees appears to be independent of distance from forest, although this might become a significant factor on trees that are more isolated than those studied here. Ant species richness on pasture trees is higher if the trees are large, support a high epiphyte load and are native to the area. Isolated trees within the agricultural matrix therefore play some role in conserving elements of the original forest ant fauna. Since some of the species on pasture trees have been observed to reach dominant or sub-dominant status in nearby forest and cocoa farms, they may play some role in limiting pest outbreaks in the pasture close to the trees. If this is so, there may be a case for retaining an adequate density of trees to enable the influence of arboreal ants to extend over as much pasture as possible.

Key words: Rain forest, fragmentation, isolation, ants, trees.

Introduction

As with other ecosystems throughout the World, Atlantic rain forest has not escaped the problems of clearing and fragmen-

tation. It once occupied about one million square kilometers of the eastern part of Brazil, but less than 9% of this ecosystem remains (Câmara, 1991) and much of it that still exists is represented in small fragments and linear strips of vegetation (Fonseca, 1985). These fragments of forest within the matrix of agricultural land are often the only means for conserving representatives of the original biota (e.g., Saunders et al., 1987).

Unfortunately fragments are prone to edge effects, such as changes in microclimate, vegetation structure and diversity, and weed invasion, all of which influence the vertebrate and invertebrate fauna (Turner, 1996; Didham, 1997). Majer et al. (1997) sampled the litter ant fauna along transects running through Atlantic rain forest into an adjacent grassland. Their findings suggested that species richness was lowest in the field and highest at the deepest point within the forest, and that certain ant species had preferences for the field or particular distances into the forest. However, it was concluded that although the ant fauna of Atlantic rain forest is severely affected by clearing, provided it is protected from degradation by a robust fence, a forest-like ant fauna is able to persist right up to the interior edge of the forest. These findings suggest that relatively small remnants of forest (1000 × 400 m in this case) can contribute to the conservation of ant communities and probably of other invertebrate groups, such as butterflies (see Brown and Brown, 1992).

In addition to the many small fragments of forest that remain, the pasture is often scattered with isolated trees that have been planted, have recolonized or are survivors from the forest that formerly occupied the area. This paper investigates the capacity of these isolated trees to support representatives of the original Atlantic rain forest ant communities and also how these arboreal ants interact with the disturbance-associated ant fauna of the pasture beneath them.

Methods

Selection and characterization of trees

Field work was carried out in February 1998 on the grounds of the Center for Cocoa Research (CEPLAC), Itabuna, Bahia (14°45'S, 39°13'W) at the same site where Majer et al. (1997) investigated the influence of forest edges on ant community structure. The grounds are predominantly planted to cocoa, although some areas are maintained as grassland. A rectangular shaped botanical reserve of secondary rain forest, measuring about 400 m × 1000 m, exists within the grounds and adjoins a field on the southern side. Despite the fact that cows were present in the field, the grass and shrubs were at least 60 cm high and litter consisted almost solely of decaying grass material. This grassland measures 700 m × 1000 m and is flanked on both eastern and western sides by more cleared land. It contained about 100 trees, scattered in a random distribution. With few exceptions, trees were at least 20 m from the neighboring tree.

Twenty trees, representing a range of distances (10–275 m) from the forest, were sampled in the grassland. Ten trees within the forest were also sampled. All selected forest trees were from within the area studied by Majer et al. (1997) and were at least 20 m from the border in order to minimize edge effects. Within the forest it was not possible to sample from the canopy of a single tree as the canopies of adjacent trees were inter-twined. Therefore samples from the forest represent a portion of continuous canopy rather than a single tree. Each tree was identified, noted as exotic or local and, for trees in the grassland, the height, crown diameter and distance of each tree from the forest was recorded. The shrub layer beneath the grassland trees was measured on a four-point scale: 1, equal to grassland; 2, grass plus up to five emergent shrubs; 3, grass plus six to twenty emergent shrubs; and 4, understorey mostly dicotyledonous shrubs. Similarly, the epiphyte load on trees was recorded as: 1, none; 2, one to five per tree; 3, six to twenty per tree; and 4, over twenty per tree. No measurements were made on the forest trees, although all had medium to dense epiphyte loads and the general height of the forest overstorey was measured as 18–20 m.

Ant sampling

In the grassland, litter ants were sampled by two complementary methods at distances of 1 m and 5 m from the tree trunk, both in the northerly and southerly direction. These samples were considered to represent the ground fauna respectively under and outside the influence of the tree and its associated arboreal ant community. Quadrats (1.0 × 0.5 m) of litter were taken at each sample point between 08:30 h–11:00 h and sieved to concentrate fine organic fragments and associated animals. For each tree, the north and south samples at a given trunk distance were combined and placed in Winkler sacks (see Besuchet et al., 1987) and hung in a room at about 28 °C for 4 days to extract ants and other invertebrates. A 75 mm internal diameter pitfall trap, containing water plus a drop of detergent, was established adjacent to each litter sampling point and left for 48 h. The fauna beneath the trees in the forest was sampled in an identical fashion, except that samples were only taken 1 m from the trunk – samples taken at greater distances fell under the influence of adjacent trees and thus did not provide an opportunity to investigate the influence of distance from tree.

Tree canopy samples were taken in mid-morning by manually collecting ants from tree trunks for a 5 minute period followed by chemical knockdown of the canopy. The latter was performed by placing a 5 m × 5 m calico sheet around the trunk. The tree was then sprayed with a motorized knapsack mistblower which delivered 3 L of pesticide (0.08 g/L Deltamethrin plus 1.66 g/L Fenthion) to the trunk and lower 7 m of the canopy of each tree. The sheets were left for at least 2 hours and all ants were removed with forceps and placed in 70% ethanol.

All ants from the Winkler sacks, pitfall traps, trunk collections and chemical knockdown were sorted to morphospecies level, identified to genus and, when possible, to species using the reference collection in

the Myrmecology Laboratory at CEPLAC. The nomenclature follows Bolton (1995). A full reference collection for this material is deposited at CEPLAC.

Weather conditions were generally sunny during much of the sampling period; 1.9 mm rain fell on one night during this time and daily maximum temperatures averaged 26.7 °C.

Data analysis

The ant species obtained in both Winkler samples ($n = 2$) and both pitfall traps ($n = 2$) situated at the same distance from the trunk of each tree were combined ($n = 4$) to provide a comprehensive assessment of the ant species found at 1 m and 5 m from the trunk of each tree. The hand collections and knockdown samples from each tree were also combined in order to provide an assessment of the ant species found on each tree.

A matrix of ant species on and beneath each tree was first prepared and used to compile lists of the frequency of ants on and beneath trees, out of 20 and 10 for pasture and forest respectively. This enabled comparisons to be made between both species richness and the actual ant species present on forest *versus* pasture trees and also on trees *versus* the ground beneath. In order to provide an indication of the relationships between ant species richness on trees with tree environmental characteristics, simple parametric correlations were performed on the ant *versus* environmental parameters. Interrelationships between the various tree and ground characteristics were also investigated by this method to see if any were interrelated. The relationship between tree and ground ant species richness was also investigated by simple correlation. Unless otherwise indicated, all correlations were performed on the pasture trees alone, since the forest trees were likely to present a discontinuity in the data.

The species presence/absence data for each of the pasture and forest trees were then ordinated (principal coordinates analysis) using the SYN-TAX[®] computer package (Podani, 1995). Sorensen's similarity index was used, as it has been shown to be one of the most reliable measures for use with binary sets of data (Huhta, 1979). Tree environmental parameters were plotted on the ordination diagram to identify whether any of these might explain differences in ant community composition.

Results

Tree characteristics

The tree species that were sampled in pasture and adjoining forest, and also their environmental characteristics, are shown in Table 1. All but one of the forest trees were indigenous to the local rain forest, although half of the pasture trees were exotic and had probably been planted as shade trees at the time of pasture establishment. Whether the indigenous trees in the pasture are regrowth or survivors from the cleared forest is unknown.

Arboreal ants

Appendix 1 shows the 125 species of ants that were sampled during this study. A full matrix of ant species by plot and method with which they were sampled may be obtained by writing to the senior author. Seventy-seven of the species were found on trees (Table 2), 48 of which were also found on the ground. Some of these species, such as *Solenopsis saevissima*, *Labidus praedator* and *Gnamptogenys striatula*

Table 1. List of tree species sampled in the pasture and forest, showing the height and crown diameter, the distance from forest edge, the epiphyte load and the understorey density of the pasture species

Tree number	Family	Species	Distance from forest (m)	Height (m)	Crown diameter (m)	Epiphyte load +	Shrub density +
P1	Bignoniaceae	<i>Tabebuia impetiginosa</i>	27	10.9	9.9	2	1
P2	Fabaceae	<i>Erethrina velutina</i> *	68	10.1	7.9	1	1
P3	Rubiaceae	<i>Genipa americana</i> *	46	14.6	9.4	1	0
P4	Fabaceae	<i>Poecilanthe ulei</i>	36	9.1	6.2	1	1
P5	Mimosaceae	<i>Inga edulis</i>	10	16.5	21.2	3	3
P6	Mimosaceae	<i>Inga edulis</i>	60	14.5	13.8	2	3
P7	Mimosaceae	<i>Inga edulis</i>	54	17.8	17.2	3	2
P8	Mimosaceae	<i>Inga edulis</i>	64	14.8	19.4	3	2
P9	Mimosaceae	<i>Inga edulis</i>	103	21.1	21.1	3	3
P10	Fabaceae	<i>Erythrina fusca</i> *	154	20.9	15.8	3	1
P11	Mimosaceae	<i>Inga edulis</i>	111	17.5	21.1	0	2
P12	Mimosaceae	<i>Inga edulis</i>	137	11.5	14.1	3	0
P13	Fabaceae	<i>Erythrina fusca</i> *	215	17.1	13.4	0	3
P14	Fabaceae	<i>Clitoria fairchildiana</i> *	189	10.5	9.4	1	2
P15	Fabaceae	<i>Clitoria fairchildiana</i> *	179	15.4	16.0	0	3
P16	Fabaceae	<i>Clitoria fairchildiana</i> *	131	13.3	12.4	0	2
P17	Rubiaceae	<i>Genipa americana</i> *	179	14.7	13.0	2	1
P18	Fabaceae	<i>Clitoria fairchildiana</i> *	228	10.0	11.6	1	3
P19	Moraceae	<i>Artocarpus heterophyllus</i>	258	7.7	5.8	1	1
P20	Fabaceae	<i>Clitoria fairchildiana</i> *	275	8.1	10.4	1	2
F1	Meliaceae	<i>Guarea macrophylla</i>	—	—	—	—	—
F2	Mimosaceae	<i>Inga edulis</i>	—	—	—	—	—
F3	Meliaceae	<i>Guarea macrophylla</i>	—	—	—	—	—
F4	Fabaceae	<i>Machaerium angustifolium</i>	—	—	—	—	—
F5	Fabaceae	<i>Erythrina fusca</i> *	—	—	—	—	—
F6	Meliaceae	<i>Guarea macrophylla</i>	—	—	—	—	—
F7	Mimosaceae	<i>Inga edulis</i>	—	—	—	—	—
F8	Mimosaceae	<i>Inga edulis</i>	—	—	—	—	—
F9	Mimosaceae	<i>Inga edulis</i>	—	—	—	—	—
F10	Flacoutiaceae	<i>Caseara</i> sp.	—	—	—	—	—

* Denote exotic species.

+ Scoring of epiphyte load and shrub density is explained in the text.

are obligate ground nesters which have foraged up on to the trees. An additional 48 species were exclusively sampled on the ground (Table 2); many of these are believed to be soil or ground nesting species, although some arboreal species, such as *Zacryptocerus pallens* and *Leptothorax spininodis* appear in this list because sampling failed to detect them on trees. Because of the serendipitous sampling of certain species, the categorization of species as arboreal, ground dwelling, or both, can only be seen as a guide. Most of the ground-living ants of this area have already been discussed by Majer et al. (1997), so this component of the fauna will not be considered in detail here.

Generally higher numbers of species were sampled on forest (mean of 14.1 species per tree) than pasture trees (9.8) ($t = -2.85$, $df = 22$, $p < 0.01$ using unpaired t-test). Comparison of richness values in forest and pasture should be approached with the realization that half as many trees were sampled in the forest. Nevertheless, 14 species were only sampled on forest trees, while 26 species were only sampled on the pasture trees; 37 species were found on both forest and pasture trees (Table 2).

Factors influencing richness of arboreal ants in pasture

Any influences on richness within the pasture can only be looked at in an indicative way since there are insufficient degrees of freedom in the data for detailed multivariate regression analyses. Table 3 shows the correlation coefficients between the various measured tree and understorey variables and also between these and ant species richness.

Tree height and crown diameter were strongly correlated. There was a significant increase in epiphyte load and in the density of shrubs beneath the trees as crown diameter increased. Epiphyte load significantly declined with increasing distance from forest, a trend that was apparently independent of tree size, which showed no trend with increasing distance from the forest margin. Arboreal ant richness significantly increased with tree height, crown diameter, epiphyte load and shrub density. The last-mentioned correlation may have resulted from the intercorrelation between tree size and shrub density. There was no decline in ant species richness with increasing distance from the forest, even when partial correlations to remove the effect of tree size were performed.

Table 2. List of ant species sampled in trees, showing which species on trees were (a) confined to forest, (b) confined to pasture, or (c) common to both habitats. Species which were only found on the ground (d) in forest and pasture are also shown

Species on trees					
(a) Forest only	(b) Pasture only	(c) Forest and pasture	(d) Species confined to ground	Forest	Pasture
<i>Acanthognathus brevicornis</i>	<i>Azteca</i> cf. <i>paraensis bondari</i>	<i>Azteca</i> cf. <i>chartifex spiriti</i>	<i>Acromyrmex subterraneus brunneus</i>	–	+
<i>Brachymyrmex</i> sp. 2	<i>Brachymyrmex</i> sp. 1	<i>A.</i> cf. <i>muelleri</i>	<i>Apterostigma</i> sp. gp. <i>pilosus</i>	+	–
<i>Camponotus itheringi</i>	<i>B.</i> sp. 3	<i>A.</i> sp. gp. <i>fasciata</i>	<i>Camponotus cingulatus</i>	+	–
<i>Ca.</i> sp. #171	<i>Camponotus atriceps</i>	<i>Camponotus bidens</i>	<i>Ca. melanoticus</i>	–	+
<i>Dendromyrmex chartifex</i>	<i>Ca. balzani</i>	<i>Ca. crassus</i>	<i>Ectatomma permagnum</i>	–	+
<i>Ectatomma tuberculatum</i>	<i>Ca. sexguttatus</i>	<i>Ca. divergens</i>	<i>Hypoponera</i> sp. 1	+	+
<i>Gnamptogenys striatula</i>	<i>Ca. trapezoides</i>	<i>Ca. godmani</i>	<i>H.</i> sp. 2	+	+
<i>Pachycondyla carinulata</i>	<i>Crematogaster brevispinosa</i>	<i>Ca. novogranadensis</i>	<i>H.</i> sp. 3	–	+
<i>Pac. unidentata</i>	<i>Cr. curvispinosa</i>	<i>Cephalotes atratus</i>	<i>H.</i> sp. 4	+	+
<i>Pheidole</i> sp. 1	<i>Cr. (Orthocrema)</i> sp. 5	<i>Crematogaster acuta</i>	<i>Labidus coecus</i>	+	+
<i>Procryptocerus adlerzi</i>	<i>Cr.</i> sp. nr. <i>quadriformis</i>	<i>Cr. limata</i>	<i>Leptogenys arcuata</i>	–	+
<i>Pseudomyrmex urbanus</i>	<i>Labidus praedator</i>	<i>Cyphomyrmex transversus</i>	<i>Leptothorax spininodis</i>	–	+
<i>Solenopsis (Diplorhoptrum)</i> sp. #47	<i>Leptothorax tristani</i>	<i>Dolichoderus bidens</i>	<i>Linepithema humile</i>	–	+
<i>Zacryptocerus pavonii</i>	<i>Monomorium floricola</i>	<i>D. diversus</i>	<i>Megalomyrmex drifti</i>	+	–
	<i>Paratrechina</i> sp. 2	<i>D. lutosus</i>	<i>Myocepurus smithii</i>	–	+
	<i>Pheidole</i> sp. #848	<i>Odontomachus haematodus</i>	<i>Myrmicocrypta</i> sp. nr. <i>buenzlii</i>	+	–
	<i>Pseudomyrmex elongatus</i>	<i>Pachycondyla crenata</i>	<i>Octostruma petiolata</i>	+	–
	<i>Ps. filiformis</i>	<i>Pac. villosa</i>	<i>Oc. rugifera</i>	+	–
	<i>Ps. laevifrons</i>	<i>Paratrechina</i> sp. 1	<i>Oc. stenognatha</i>	+	–
	<i>Ps. simplex</i>	<i>Pheidole</i> sp. 2	<i>Pachycondyla apicalis</i>	+	–
	<i>Ps.</i> sp. gp. <i>pallidus</i> #809	<i>Procryptocerus hirsutus</i>	<i>Pac. constricta</i>	+	–
	<i>Ps.</i> sp. gp. <i>pallidus</i>	<i>Pr. hylaeus</i>	<i>Pac. harpax</i>	+	+
	<i>Solenopsis (Diplorhoptrum)</i> sp. 2	<i>Pr. spiniperdus</i>	<i>Paratrechina</i> sp. 3	+	+
	<i>So. saevissima</i>	<i>Pseudomyrmex cubaensis</i>	<i>Par.</i> sp. 4	–	+
	<i>Strumigenys subdentata</i>	<i>Ps. euryblemma</i>	<i>Pheidole fimbriata</i>	+	–
	<i>Wasmannia</i> sp. #270	<i>Ps. gracilis</i>	<i>Ph.</i> sp. 188	–	+
		<i>Ps. rochai</i>	<i>Ph.</i> sp. 3	+	+
		<i>Ps. sericeus</i>	<i>Ph.</i> sp. 4	–	+
		<i>Ps. spiculus</i>	<i>Ph.</i> sp. 5	–	+
		<i>Ps. tenuis</i>	<i>Ph.</i> sp. 6	+	–
		<i>Ps. tenuissimus</i>	<i>Ph.</i> sp. 7	–	+
		<i>Wasmannia auropunctata</i>	<i>Ph.</i> sp. nr. <i>laevifrons</i>	–	+
		<i>Zacryptocerus goeldii</i>	<i>Prionopelta antillana</i>	+	+
		<i>Za. maculatus</i>	<i>Rhopalothrix</i> sp. n	+	–
		<i>Za. minutus</i>	<i>Rogeria besucheti</i>	–	+
		<i>Za. simillimus</i>	<i>Ro. foreli</i>	–	+
		<i>Za. umbraculatus</i>	<i>Ro. micromma</i>	–	+
			<i>Smithistruma schulzi</i>	+	+
			<i>Solenopsis (Diplorhoptrum)</i> sp. #12	+	–
			<i>So. (Diplorhoptrum)</i> sp. #25	–	+
			<i>So. (Diplorhoptrum)</i> sp. 3	+	+
			<i>Strumigenys denticulata</i>	+	+
			<i>St. dolichognatha</i>	+	–
			<i>St. louisiana</i>	+	+
			<i>Tapinoma</i> sp. 1	–	+
			<i>Trachymyrmex cornetzi</i>	+	–
			<i>Wasmannia</i> sp. #778	–	+
			<i>Zacryptocerus pallens</i>	–	+
14 species	26 species	37 species	48 species		

The ordination of forest and pasture trees in terms of the presence/absence ant data is shown in Figure 1a. The forest trees were separated from most of the pasture trees on the lower left of the diagram, suggesting that trees in the two habitats support demonstrably different ant communities. Pasture trees P5, P6, P8, P9 and P11 were most similar to the forest trees in terms of their ant community composition. Similarity

to forest did not seem to be related to ant species richness, since several of the pasture trees that were separated from forest trees on the ordination supported as many species as some of those situated close to the forest grouping of trees. Factors that might have contributed to the distinctiveness of the pasture tree fauna included increasing distance from forest (Fig. 1b), declining epiphyte load (Fig. 1c), declining tree dia-

	Distance from forest	Tree height	Crown diameter	Epiphyte load	Shrub density	Ant species on tree	Ant species 1 m from trunk	Ant species 5 m from trunk
Distance from forest	–	– 0.28 ns	+ 0.14 ns	– 0.41 *	+ 0.14 ns	– 0.27 ns	+ 0.27 ns	+ 0.50 *
Tree height		–	+ 0.80 ***	+ 0.35 ns	+ 0.32 ns	+ 0.53 **	– 0.34 ns	– 0.42 *
Crown diameter			–	+ 0.41 *	+ 0.49 *	+ 0.71 ***	– 0.30 ns	– 0.11 ns
Epiphyte load				–	– 0.13 ns	+ 0.51 *	– 0.53 **	– 0.28 ns
Shrub density					–	+ 0.45 *	+ 0.32 ns	+ 0.13 ns
Ant species on tree						–	– 0.35 ns	– 0.23 ns
Ant species 1 m from trunk							–	+ 0.55 **
Ant species 5 m from trunk								–

Table 3. Correlations and their significance (* = < 0.05, ** = < 0.01, *** = < 0.001) between tree and understorey characteristics with each other and with ant species richness on trees and on the ground at 1 m and 5 m from the trunk. Calculations are performed on the pasture trees only (n = 20)

meter and increased incidence of exotic tree species (Fig. 1 d). Since many of these parameters were intercorrelated, it is not possible to discuss their relative importance.

Interaction between arboreal and ground ants

Forty-five species of ants were sampled on the ground of the forest and 74 were sampled on the ground of the pasture beneath trees. Comparison of these figures should take into account the higher number of trees sampled in the pasture and the fact that two distances from the tree were sampled in the pasture, but only one in the forest. If only the 1 m position beneath trees is compared, the richness of ants does not differ on the ground beneath pasture and forest trees (mean of 9.9 and 8.7 for base of forest and pasture trees respectively; $p > 0.05$ using unpaired t-test).

In the forest, 13 species (25.4%) of the ants sampled on trees were also found on the ground (Table 4). On the basis of knowledge of their ecology, nesting habits, and their frequency on trees versus ground beneath trees (Table 4), several of these are considered to be arboreal species that may also forage on the ground or species that nest in substrates that are common to both ground and trees. The only obligate soil nesting species sampled on the forest trees was *Gnamptogenys striatula*. The proportion of ants that were sampled on pasture trees that were also sampled on the ground beneath was much higher (41 species, 65.1% overlap between trees and ground). At least two soil nesting species, *Solenopsis saevissima* and *Pseudomyrmex tenuis*, and also the army ant, *Labidus praedator*, were found on the pasture trees. The list of pasture tree ants also contained a greater

proportion of species that are able to use both ground and arboreal substrates for nesting than did the forest list. This is further illustrated by the fact that 11 of the species found on pasture trees were more frequent in the ground samples than on the trees, whereas the corresponding figure for the forest was six (Table 4).

Twenty-one of the species on pasture trees were only sampled 1 m from the trunk, while a further 20 were sampled up to 5 m from the trunk (Table 4). Many of the species confined to 1 m from the trunk were either arboreal species that may forage on the ground or species with broad nesting habits; only two species in this group were more frequent on the ground than on the trees. By contrast, those which were also found 5 m from the trunk included a higher proportion of ground nesters that foraged on trees or species with broad nesting habits; nine of these species were more frequent on the ground than on trees (Table 4). One consequence of this overlap between tree and ground ants was that richness was higher immediately adjacent to trunk (mean 8.7 species) than 5 m from the trunk (mean 6.7 species) ($t = 2.73$, $df = 19$, $p < 0.013$ using paired t-test). There was a significant positive correlation between the number of species 1 m and 5 m from the trunk (Table 3), suggesting that the “halo” of richness close to trunks may extend out to at least 5 m, albeit with a diminished magnitude. When the enriching effect of trees on the ant fauna at 1 m from the trunk was removed, the contrast between ground ant richness of forest (mean of 9.9 species) and pasture (mean of 6.7 species at 5 m from trunk) was high and significantly different ($t = 2.30$, $df = 15$, $p < 0.05$ using unpaired t-test), a trend already pointed out by Majer et al. (1997).

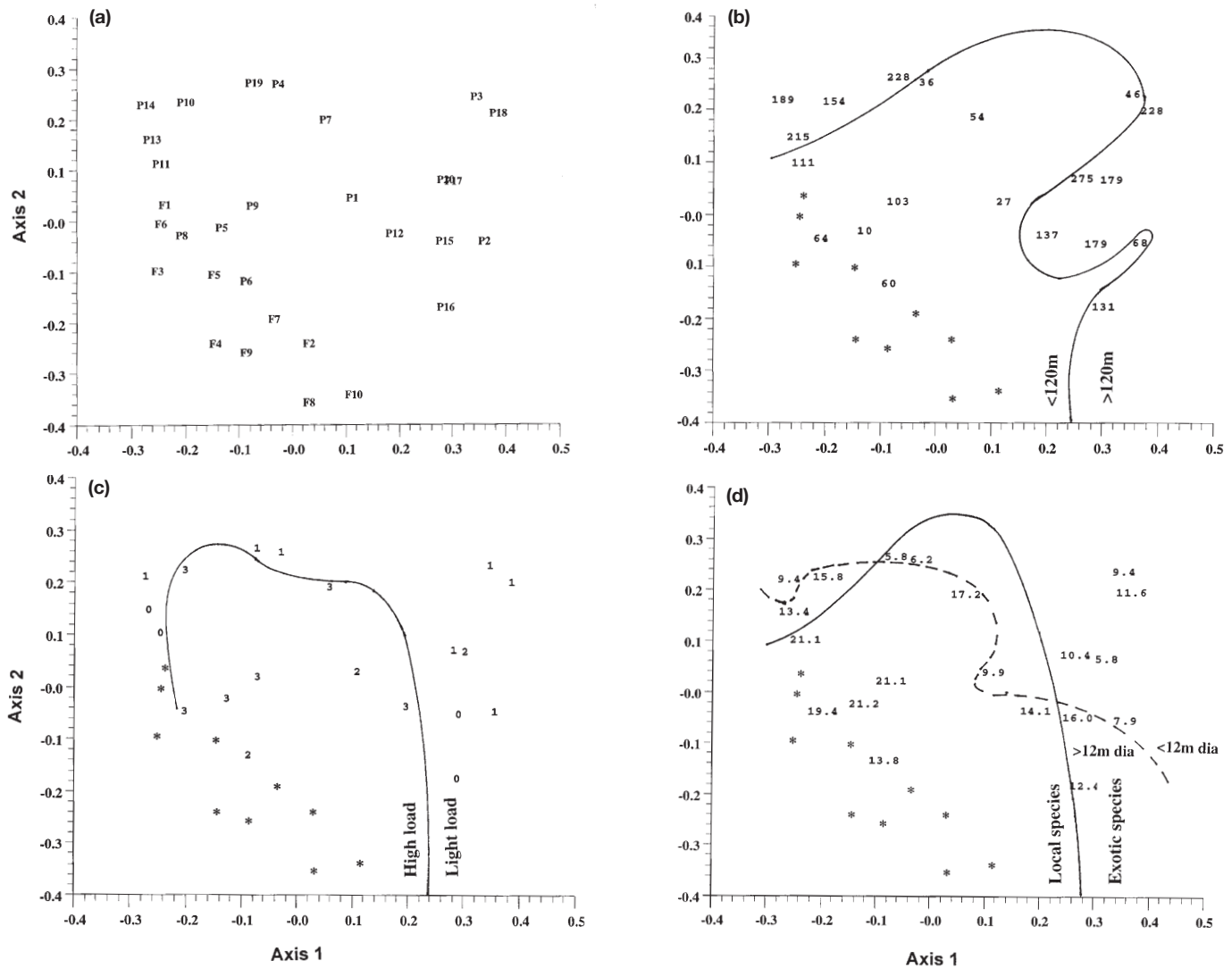


Figure 1. First and second axes of the principal coordinates ordination of forest and pasture trees (a) using ant presence/absence data, showing possible relationships between ant community composition on trees with (b) distance from forest, (c) epiphyte load, (d) tree crown diameter and whether or not the trees were local species. Forest trees are represented by asterisks in (b), (c) and (d)

While ground ant species richness (5 m from trunk) increased significantly with increasing distance from forest, it declined with increasing tree height (at 5 m from trunk) and epiphyte load (at 1 m from trunk) (Table 3). Although these are virtually the reverse of correlations between arboreal ants with habitat variables, this relationship may partially operate through the influence of arboreal ants on ground ant richness. However, the extent of this influence does not appear to be high, since the negative correlation between tree ant richness and ground ants 5 m from the trunk is not significant. Further evidence that arboreal ants are exerting little or no influence on the ground fauna stems from the fact that richness of ground-associated species was higher 1 m from the trunk (7.3 species) than 5 m away (5.7 species) ($t = -2.28$, $df = 19$, $p < 0.05$ using paired t-test).

Discussion

Pasture trees support a high richness of arboreal ant species. The incidence of such species raises the richness of ants in a 'halo' of ground beneath the trees, although there is some evidence that it may reduce the variety of ground-associated ants close to the trunk. However, there is also the possibility that there are no interactions between arboreal and ground species; each guild of ants may be responding independently to changing habitat/environmental conditions with distance from tree. The communities of arboreal ants on pasture trees are somewhat different from those in the forest. Some of these differences may be explained by serendipitous sampling of species. However, our knowledge of the local ant fauna suggests that some of the species found on pasture trees

Table 4. Species of ants sampled on trees in (a) forest and (b) pasture that were also sampled on the ground at either 1 m or 5 m (pasture only) from the trunk. Numbers in columns are frequency out of 10 (forest) or 20 (pasture)

(a) Ants on forest trees				(b) Ants on pasture trees								
				Up to 1 m from trunk				Up to 5 m from trunk				
	Tree	Ground	Nesting	Tree	Ground	Nesting	Tree	Ground	Ground	Nesting		
	(1 m)	(1 m)	habit	(1 m)	(1 m)	habit	(1 m)	(1 m)	(5 m)	habit		
<i>Azteca cf. chartifex spiriti</i>	2	1	a,n	<i>Azteca cf. chartifex spiriti</i>	9	1	a,n	<i>Brachymyrmex</i> sp.1	1	1	6	?b,s
<i>A. cf. muelleri</i>	3	1	a,c	<i>Brachymyrmex</i> sp.3	1	3	?b,s	<i>Camponotus atriceps</i>	1	2	1	c,e,l
<i>Crematogaster acuta</i>	2	2	a,c,r	<i>Camponotus balzani</i>	4	1	a,e	<i>Ca. crassus</i>	8	1	1	s,c,t
<i>Cr. limata</i>	5	3	a,e,r	<i>Ca. bidens</i>	4	1	a	<i>Ca. novogranadensis</i>	4	3	2	s,c,t
<i>Cyphomyrmex transversus</i>	2	2	t	<i>Ca. trapezoideus</i>	2	1	a	<i>Ca. sexguttatus</i>	2	0	1	a,v
<i>Gnamptogenys striatula</i>	1	2	s	<i>Crematogaster curvispinosa</i>	2	1	a	<i>Cephalotes atratus</i>	5	0	1	a,c
<i>Odontomachus haematodus</i>	6	7	s,t,l	<i>Cr. limata</i>	4	2	a,e,r	<i>Crematogaster acuta</i>	1	0	1	a,c,r
<i>Pachycondyla villosa</i>	4	1	a,c	<i>Dolichoderus diversus</i>	3	1	a,e	<i>Cr. brevispinosa</i>	7	2	2	a,?c
<i>Paratrechina</i> sp. 1	1	2	a,?l	<i>D. lutosus</i>	3	1	a,e	<i>Cr. sp. nr. quadriformis</i>	5	3	5	a,?c
<i>Pheidole</i> sp. 1	2	3	?b	<i>Leptothorax tristani</i>	1	1	a	<i>Cyphomyrmex transversus</i>	2	7	5	t
<i>Ph. sp. 2</i>	2	2	?b	<i>Paratrechina</i> sp. 2	1	2	a,b,?t	<i>Dolichoderus bidens</i>	4	1	2	a,v
<i>Solenopsis (Diplorhoptrum)</i> sp. #47	3	8	b,l	<i>Pheidole</i> sp. 2	2	1	?b	<i>Labidus praedator</i>	1	7	5	y
<i>Wasmannia auropunctata</i>	2	8	l,b,t	<i>Procrytocerus hirsutus</i>	3	1	a,t	<i>Monomorium floricola</i>	6	12	4	b,l
				<i>Pseudomyrmex cubaensis</i>	2	1	a,t	<i>Odontomachus haematodus</i>	6	12	11	s,t,l
				<i>Ps. elongatus</i>	6	2	a,t	<i>Pachycondyla crenata</i>	3	0	1	a
				<i>Ps. gracilis</i>	12	1	a,t	<i>Paratrechina</i> sp. 1	2	5	2	a,?l
				<i>Ps. sp. gp. pallidus</i>	2	1	a,t	<i>Solenopsis (Diplorhoptrum)</i> sp. 2	4	4	1	l
				<i>Ps. tenuis</i>	2	2	s	<i>So. saevissima</i>	1	8	5	s
				<i>Wasmannia</i> sp. #270	1	1	a,e	<i>Strumigenys subdentata</i>	2	7	3	t,?l
				<i>Zacryptocerus goeldii</i>	10	1	a,t	<i>Wasmannia auropunctata</i>	4	13	8	l,b,t
				<i>Za. minutus</i>	7	1	a,t					

a : tree nesting species

b : species nesting under tree bark

c : species nesting in wood cavities

e : species nesting in or on epiphytes

l : species nesting in leaf litter

n : species constructing carton-like nests

r : species nesting in arboreal termite nests

s : species nesting in soil

t : nesting in hollow twigs or decaying vegetation on tree or ground

v : species nesting on live leaves

y : army ants

Note that apparent discrepancies between categorization of ant species here and in Table 2 result from some species being present on trees but not on the ground in either forest or pasture.

are adapted to open conditions (e.g., *Camponotus novo-granadensis*, *C. sexguttatus*, *Pseudomyrmex tenuis*, *Wasmannia* sp. #270) or are disturbance specialists (e.g., *Solenopsis saevissima*, *Wasmannia auropunctata*).

Provided the tree is suitable for occupation by a variety of ants, the richness of ants appears to be independent of distance from forest within the investigated range of 10–275 m. The weak distance effects that we did observe may in part have resulted from the tendency of trees situated furthest from the forest to be exotic species with low epiphyte loads. All of the trees we sampled were within a relatively short distance from the forest edge. At this stage we are not sure if such high diversities are found on trees that are more isolated from colonizing sources. We were unable to examine this in this part of Bahia since it is a cocoa growing area, where pastures are generally close to cocoa farms that support a forest-like ant fauna. Areas such as the State of Espírito Santo, where forest has largely been cleared for grassland, would provide a suitable opportunity to examine the effect of greater distances from forest.

This research indicates how isolated trees within the agricultural matrix play a role in conserving elements of the original forest ant fauna. Furthermore, the conservation potential of such trees is enhanced if the trees are large, support a high epiphyte load and are native to the area. Such trees are more likely to contain the variety of nesting sites listed in Table 4 and more feeding opportunities than the smaller, or exotic, trees which may have been deliberately planted in the pasture. Additionally, the larger the tree, the more it is able to buffer the microclimate within and beneath the canopy; although not measured, temperatures below larger trees in this study were noticeably lower than beneath smaller trees. It seems reasonable to expect that trees which support a rich, forest-like, ant fauna may support a wide variety of other invertebrate taxa. Recent work in Mexico (Guevara et al., 1996) has also shown that isolated forest trees are able to support a wide range of frugivorous birds and that a forest understorey is encouraged beneath these trees by seed dropped in the faeces of such birds. Thus retention of trees in pastures in places where the rehabilitation of forest is impracticable should be encouraged in order to complement the conservation of both invertebrates and vertebrates in the remaining Atlantic rain forest. Such trees may also act as a network of islands and stepping stones that allow some species to maintain and spread their distribution across the landscape. Although this may appear to be a poor substitute for adequate reservation of forest, it may play a significant role in landscapes where, in some States, up to 99% of the forest has been cleared (CIMA, 1991).

Some ant species on pasture trees have been observed to reach dominant or sub-dominant status (for a definition of these concepts, see Majer et al., 1994) in nearby forest and cocoa farms (e.g., *Azteca paraensis bondari*, *A. chartifex spiriti*, certain *Crematogaster* spp., *Dolichoderus bidens*, *Wasmannia auropunctata* and *Cephalotes atratus*) (Leston, 1978; Winder, 1978; Majer and Delabie, 1993; Majer et al., 1994). There is evidence from cocoa plantations in the same region that dominant arboreal species may be active on the

ground around their host trees (Delabie et al., 1999). Since this numerically dominant group of ants has the potential to reduce the levels of arthropods, they may play some role in limiting pest outbreaks in the pasture close to the trees. If this is so, there may be a case for retaining and planting trees to enable the influence of arboreal ants to extend over as much pasture as possible.

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Appendix 1. Taxonomic list of ant species sampled on pasture and forest trees and on the ground beneath them.

Subfamily	Species	Subfamily	Species
Ponerinae	<i>Ectatomma permagnum</i> Forel	Myrmicinae	<i>Pheidole</i> sp. #848
Ponerinae	<i>Ectatomma tuberculatum</i> (Olivier)	Myrmicinae	<i>Pheidole</i> sp. nr. <i>laevifrons</i> Mayr
Ponerinae	<i>Gnamptogenys striatula</i> Mayr	Myrmicinae	<i>Procrystocerus adlerzi</i> (Mayr)
Ponerinae	<i>Hypoponera</i> sp. 1	Myrmicinae	<i>Procrystocerus hirsutus</i> Emery
Ponerinae	<i>Hypoponera</i> sp. 2	Myrmicinae	<i>Procrystocerus hylaeus</i> Kempf
Ponerinae	<i>Hypoponera</i> sp. 3	Myrmicinae	<i>Procrystocerus spiniperdus</i> Forel
Ponerinae	<i>Hypoponera</i> sp. 4	Myrmicinae	<i>Rhopalothrix</i> sp. n
Ponerinae	<i>Leptogenys arcuata</i> Roger	Myrmicinae	<i>Rogeria besucheti</i> Kugler
Ponerinae	<i>Odontomachus haematodus</i> (L.)	Myrmicinae	<i>Rogeria foreli</i> Emery
Ponerinae	<i>Pachycondyla apicalis</i> (Latreille)	Myrmicinae	<i>Rogeria micromma</i> Kempf
Ponerinae	<i>Pachycondyla carinulata</i> (Roger)	Myrmicinae	<i>Smithistruma schulzi</i> (Emery)
Ponerinae	<i>Pachycondyla constricta</i> (Mayr)	Myrmicinae	<i>Solenopsis (Diplorhoptrum)</i> sp. #47
Ponerinae	<i>Pachycondyla crenata</i> (Roger)	Myrmicinae	<i>Solenopsis (Diplorhoptrum)</i> sp. 2
Ponerinae	<i>Pachycondyla harpax</i> (Fabricius)	Myrmicinae	<i>Solenopsis (Diplorhoptrum)</i> sp. 3
Ponerinae	<i>Pachycondyla unidentata</i> (Mayr)	Myrmicinae	<i>Solenopsis (Diplorhoptrum)</i> sp. #25
Ponerinae	<i>Pachycondyla villosa</i> (Fabricius)	Myrmicinae	<i>Solenopsis (Diplorhoptrum)</i> sp. #12
Ponerinae	<i>Prionopelta antillana</i> Forel	Myrmicinae	<i>Solenopsis saevissima</i> (Smith)
Ecitoninae	<i>Labidus coecus</i> (Latreille)	Myrmicinae	<i>Strumigenys denticulata</i> Mayr
Ecitoninae	<i>Labidus praedator</i> (Smith)	Myrmicinae	<i>Strumigenys dolichognatha</i> Weber
Pseudomyrmecinae	<i>Pseudomyrmex cubaensis</i> (Forel)	Myrmicinae	<i>Strumigenys louisianae</i> Roger
Pseudomyrmecinae	<i>Pseudomyrmex elongatus</i> (Mayr)	Myrmicinae	<i>Strumigenys subedentata</i> Mayr
Pseudomyrmecinae	<i>Pseudomyrmex euryblemma</i> Forel	Myrmicinae	<i>Trachymyrmex cornetzi</i> Forel
Pseudomyrmecinae	<i>Pseudomyrmex filiformis</i> (Fabricius)	Myrmicinae	<i>Wasmannia auropunctata</i> (Roger)
Pseudomyrmecinae	<i>Pseudomyrmex gracilis</i> (Fabricius)	Myrmicinae	<i>Wasmannia</i> sp. #270
Pseudomyrmecinae	<i>Pseudomyrmex laevifrons</i> Ward	Myrmicinae	<i>Wasmannia</i> sp. #778
Pseudomyrmecinae	<i>Pseudomyrmex rochai</i> (Forel)	Myrmicinae	<i>Zacryptocerus goeldii</i> (Forel)
Pseudomyrmecinae	<i>Pseudomyrmex sericeus</i> (Mayr)	Myrmicinae	<i>Zacryptocerus maculatus</i> (Smith)
Pseudomyrmecinae	<i>Pseudomyrmex simplex</i> (Smith)	Myrmicinae	<i>Zacryptocerus minutus</i> (Fabricius)
Pseudomyrmecinae	<i>Pseudomyrmex</i> sp. gp. <i>pallidus</i> #809	Myrmicinae	<i>Zacryptocerus pallens</i> (Klug)
Pseudomyrmecinae	<i>Pseudomyrmex</i> sp. gp. <i>pallidus</i> no reg.	Myrmicinae	<i>Zacryptocerus pavonii</i> (Latreille)
Pseudomyrmecinae	<i>Pseudomyrmex spiculus</i> Ward	Myrmicinae	<i>Zacryptocerus similimus</i> (Kempf)
Pseudomyrmecinae	<i>Pseudomyrmex tenuis</i> (Fabricius)	Myrmicinae	<i>Zacryptocerus umbraculatus</i> (Fabricius)
Pseudomyrmecinae	<i>Pseudomyrmex tenuissimus</i> Ward	Dolichoderinae	<i>Azteca</i> cf. <i>chartifex spiriti</i> (Forel)
Pseudomyrmecinae	<i>Pseudomyrmex urbanus</i> (Smith)	Dolichoderinae	<i>Azteca</i> cf. <i>muelleri</i> Emery
Myrmicinae	<i>Acanthognathus brevicornis</i> Smith	Dolichoderinae	<i>Azteca</i> cf. <i>paraensis bondari</i> Borgmeier
Myrmicinae	<i>Acromyrmex subterraneus brunneus</i> Forel	Dolichoderinae	<i>Azteca</i> sp. gp. <i>fasciata</i>
Myrmicinae	<i>Apterostigma</i> sp. gp. <i>pilosus</i>	Dolichoderinae	<i>Dolichoderus bidens</i> (L.)
Myrmicinae	<i>Cephalotes atratus</i> (L.)	Dolichoderinae	<i>Dolichoderus diversus</i> Emery
Myrmicinae	<i>Crematogaster acuta</i> (Fabricius)	Dolichoderinae	<i>Dolichoderus lutosus</i> (Smith)
Myrmicinae	<i>Crematogaster brevispinosa</i> Mayr	Dolichoderinae	<i>Linepithema humile</i> (Mayr)
Myrmicinae	<i>Crematogaster curvispinosa</i> Mayr	Dolichoderinae	<i>Tapinoma</i> sp. 1
Myrmicinae	<i>Crematogaster limata</i> Smith	Formicinae	<i>Brachymyrmex</i> sp. 1
Myrmicinae	<i>Crematogaster (Orthocrema)</i> sp. 5	Formicinae	<i>Brachymyrmex</i> sp. 2
Myrmicinae	<i>Crematogaster</i> sp. nr. <i>quadriformis</i>	Formicinae	<i>Brachymyrmex</i> sp. 3
Myrmicinae	<i>Cyphomyrmex transversus</i> Emery	Formicinae	<i>Camponotus atriceps</i> (Smith)
Myrmicinae	<i>Leptothorax spininodis</i> Mayr	Formicinae	<i>Camponotus balzani</i> Emery
Myrmicinae	<i>Leptothorax tristani</i> (Emery)	Formicinae	<i>Camponotus bidens</i> Mayr
Myrmicinae	<i>Megalomyrmex drifti</i> Kempf	Formicinae	<i>Camponotus cingulatus</i> (Mayr)
Myrmicinae	<i>Monomorium floricola</i> (Jerdon)	Formicinae	<i>Camponotus crassus</i> Mayr
Myrmicinae	<i>Mycocepurus smithii</i> Forel	Formicinae	<i>Camponotus divergens</i> Mayr
Myrmicinae	<i>Myrmicocrypta</i> sp. nr. <i>buenzlii</i>	Formicinae	<i>Camponotus godmani</i> Forel
Myrmicinae	<i>Octostruma petiolata</i> (Mayr)	Formicinae	<i>Camponotus iheringi</i> Forel
Myrmicinae	<i>Octostruma rugifera</i> (Mayr)	Formicinae	<i>Camponotus melanoticus</i> Emery
Myrmicinae	<i>Octostruma stenognatha</i> Brown & Kempf	Formicinae	<i>Camponotus novogranadensis</i> Mayr
Myrmicinae	<i>Pheidole fimbriata</i> Roger	Formicinae	<i>Camponotus sexguttatus</i> (Fabricius)
Myrmicinae	<i>Pheidole</i> sp. 1	Formicinae	<i>Camponotus</i> sp. #171
Myrmicinae	<i>Pheidole</i> sp. #188	Formicinae	<i>Camponotus trapezoideus</i> Mayr
Myrmicinae	<i>Pheidole</i> sp. 2	Formicinae	<i>Dendromyrmex chartifex</i> (Smith)
Myrmicinae	<i>Pheidole</i> sp. 3	Formicinae	<i>Paratrechina</i> sp. 1
Myrmicinae	<i>Pheidole</i> sp. 4	Formicinae	<i>Paratrechina</i> sp. 2
Myrmicinae	<i>Pheidole</i> sp. 5	Formicinae	<i>Paratrechina</i> sp. 3
Myrmicinae	<i>Pheidole</i> sp. 6	Formicinae	<i>Paratrechina</i> sp. 4
Myrmicinae	<i>Pheidole</i> sp. 7		