Arboreal Ant Community Patterns in Brazilian Cocoa Farms

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ABSTRACT
The distribution of arboreal-foraging ants on cocoa trees was investigated at the Centre for Cocoa Research in Bahia, Brazil. The interactions between ant species were quantified using data on the presence or absence of ant species on 1160 cocoa trees. The distribution of ants was also mapped in four 30 x 40 m plots of cocoa, and the species richness and biomass of ants was assessed by chemical knockdowns from within the territories of five of the dominant ant species.

Ninety-one species of ant were encountered, of which seven reached dominant status. A quantitative evaluation of the number of positive and negative associations between each ant species confirmed the status of most of these dominants and also indicated that a further 10 species may have sub-dominant status. The dominants were distributed in a mosaic-like fashion and, except in an old, non-pesticide-treated cocoa plot, gaps in the mosaic were few. Some of the dominant ants influenced the number of associated ant species, the length of those ant species with which they were able to co-exist, and also the species composition of ants within their territory.

Key words: ants; biomass; Brazil; distribution; diversity; dominance; Formicidae; mosaic.

Reports of arboreal-foraging ants being distributed in a three-dimensional mosaic come from the tropical parts of Africa, e.g., in Ghanaian cocoa (Majer 1972); Asia, e.g., in Solomon Islands coconut (Greenslade 1971); Australia, e.g., in Mango (Majer & Carmel-Cesti 1991); and South America, e.g., in rain forest (Lesdon 1978). This mosaic consists of a limited number of dominant ants, which have been defined as those species which predominate numerically, which tend to have mutually exclusive distribution patterns, and which tend to occupy large and continuous expanses of forest or tree crop canopy (Lesdon 1973). Associated with this mosaic are sub-dominant ants, which are also numerous but which do not usually hold large tracts of canopy, and non-dominants, which occur within or between the territories of dominant ants. In view of the fact that certain sub-dominant and non-dominant ants tend to be associated with particular dominant ant species (Room 1971), there is a tendency for much of the ant community to be distributed in a mosaic-like fashion. Areas where dominant ants are absent from the trees are referred to as gaps, or lacunae, and such areas tend to be relatively restricted. The composition of ant mosaics throughout the tropics has recently been reviewed by Majer (1993).

Whilst working at the Centre for Cocoa Research (CEPLAC) in Bahia, Brazil, Lesdon (1978) mapped an ant mosaic in Atlantic rain forest. This comprised seven ant species which Lesdon considered as dominant, with an additional species considered to be sub-dominant. Lesdon (1978) also observed, but did not map, an ant mosaic in nearby cocoa which contained five additional dominant species. Winder (1978) mapped the occurrence of ant species on cocoa flowers at CEPLAC and noted a mosaic-like distribution pattern of various ant genera. His data did not indicate whether any of these ants were dominant or not.

In this paper we provide more detailed information on the nature of the ant mosaic in Brazilian cocoa. More specifically, we propose a quantitative method for identifying which species are dominant, and we investigate how these dominant species are distributed and how they affect the other ant species which occur within their territory. This information is important as it documents the capacity of this dominant group of animals (Fitzkauf & Klinge 1973) to influence the composition of the associated ant community. It also provides information which may be utilised in the effort to screen ant species for use in biological control programs for tropical tree crop pests. This aspect of the current study is reported elsewhere (Majer & Delabie, in press).

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METHODS

FIELD WORK.—Fieldwork was carried out within the grounds of the Centre for Cocoa Research (CEPLAC), Itabuna, Bahia, (14°45'S, 39°13'W) and formed components of several research modules directed at elucidating the possible use of ants in biological pest control programs. The results are presented in a sequence which enables an understanding of the ant mosaic to be developed rather than as a time sequence of data collection.

In order to determine whether there was any association between the various species of ants, we surveyed the species present on 1100 randomly selected trees spread throughout the CEPLAC grounds. Samples were taken between August 1990 and June 1991 by manually collecting ants from trees for a 5 minute period followed by the beating of the canopy over a 2 × 2 m sheet. Care was taken to select trees which were at least 15 m apart in order to ensure independence of samples.

Four 30 m × 40 m plots of cocoa were selected for mapping of arboreal ants. The plots were located in the centre of blocks of cocoa and were thus free of edge-effects. Plots 1, 2, and 3 were beneath planted Erythrina shade trees and were respectively of 19, 18, and 8 year old cocoa which had been regularly sprayed with carbaryl or methamidophos to minimize insect pest problems. Plot 4, containing 60 year old cocoa, differed from the rest in that it had not been treated with pesticide for over 20 years, and cocoa had been planted under partially cleared semi-deciduous rain forest. The position of the cocoa and shade trees was first mapped. Each tree was then inspected for a period of 5 minutes and representatives of all ant species on the trunk and foliage or within cavities were collected. During this period a 2 m × 2 m calico sheet was placed under the tree and the ants were dislodged from the upper canopy by beating with a long pole. Mapping of ants on Plots 1–4 was completed between 13 and 29 September 1989.

On completion of mapping, the dominant ant species in the entire block in which Plot 3 was situated were mapped between 4, 5 October 1989 (at this stage in the investigation we classified ant species as dominant using the subjective criteria outlined in the Data Analysis section). The resulting map was used to select trees for sampling by the chemical knockdown procedure. We had intended to sample 10 trees occupied by each of five dominant ant species present in this block. However, due to changes in the distribution of dominant ants in the 2–3 week interval between mapping and knock-down sampling, we finally obtained samples from five trees with Aphaenogaster antosilis, 10 with Aphaenogaster spixii, 13 with Camponotus cretaceus, nine with Ectatomma tuberculatum, and six with Wasmannia auropunctata. Knockdown sampling of canopy invertebrates was subsequently performed between 16 October and 1 November 1989. The day prior to sampling, the undergrowth beneath each tree was cleared with a machete. A 4 m × 4 m calico sheet was then placed beneath each tree, which was then sprayed with a 5 liter mixture of delta- endrin diluted to a concentration of 0.25 g liter⁻¹. After 30 minutes, the canopy was shaken to dislodge animals, and the sheets were removed to the laboratory where the invertebrates were collected and sorted to ordinal or, in the case of ants, species level. The ants and remaining invertebrates were then separately drained for 12 h in filter paper funnels. The resulting weight of the samples was considered to approximate the live weight of the animals. All collected ant material was sorted and identified to species level. In some instances it was not possible to obtain specific names so a CEPLAC ant reference collection code number was allocated to the appropriate species. A full reference collection is deposited in the Myrmecology Laboratory at CEPLAC.

DATA ANALYSIS.—We experienced some difficulty distinguishing dominant or sub-dominant ants from those species which were non-dominant. Our decisions were initially based on three subjective criteria, not all of which prevailed to each species of ant. Firstly, those species where more than 100 ants were observed foraging on trees were considered to be dominant. Secondly, those species which occupied extensive contiguous blocks of trees in the absence of other such species were also classified as dominant. A third criterion for dominance was the presence of a relatively high biomass of ants on trees.

Since a given species did not always satisfy all three criteria for dominance, we considered that a more objective means for identifying dominance was needed. The following quantitative means for detecting dominance in the ant fauna was therefore devised. The frequency on trees of each ant species surveyed in the 1100-tree survey was first calculated. Then, using only those species which occurred on >5 percent of the trees (71 species), the association between species on trees was tested by χ² analysis with Yates' correction applied. This is identical to the procedure used by Roome (1971) for the measurement of association between ants in Ghanaian cocoa. The number of times each species re-
respectively exhibited a significant \((P < 0.05)\) positive or negative association with another species was then tallied and an Index of Dominance was calculated as follows:

\[
\text{Index of Dominance (ID)} = \frac{N - P}{N + P}
\]

where \(N\) is the number of negative associations and \(P\) is the number of positive associations. The rationale behind this index is that a dominant species should exhibit a greater number of negative associations with other species, both dominant or otherwise, while the remaining species are more likely to co-exist with other species as a result of their lower densities, less aggressive behavior, and the possibility of their sharing the same habitat requirements. We do not consider the alternative outcome of a non-dominant exhibiting significant negative associations with several dominant ants to be likely because such a species would inevitably be uncommon and hence unlikely to exhibit statistically significant negative associations. In order to investigate the influence of dominant ants on other ant species, we calculated the mean number of ant species found with each dominant species in the chemical knockdown samples. The number of associated ant species were then compared by one-way analysis of variance.

An inventory of all ant species which occupied each tree within the territories of the dominant ant species, which were mapped in Plots 1–4, was then prepared and the lengths of each species was measured. The overall percentage of ant species (total = 91) which fell within each mm size-class was then calculated. This calculation was then repeated separately for those species which occurred within the territory of each dominant species whose distribution had been mapped. The observed distribution of ants by size range was then compared by \(\chi^2\) analysis with the expected size range had the co-existing ants been randomly drawn from the total pool of ants. In order to produce 'expected' cell values greater than 5, we binned the 2–3 mm, 4–6 mm and 7–11 mm size classes.

**RESULTS**

**Dominance status of ants.**—Our three subjective criteria for recognizing dominance enabled us to provisionally identify seven species of dominant ant, *Azteca chartifex sp., A. instabilis, Crematogaster limata, C. erecta, C. acuta, and W. aureopunctata* were all found in numbers greater than 100 during the 5 minute observation periods. All of the above, except *C. erecta* but with the addition of *E. tuberculatum*, tended to monopolize large contiguous blocks of canopy. Finally, in terms of high biomass, the *Azteca* spp. and *Crematogaster* spp. all satisfied the dominance criteria, due to the presence of large numbers of small ants, and *E. tuberculatum* also satisfied this criterion because the low densities of ants were offset by the large size of the workers.

Figure 1 shows the relationship between the Index of Dominance and the overall number of statistically significant positive and negative interactions recorded for each species. Although somewhat arbitrary, the diagram may be divided into three zones: ID \(< -0.8\); ID \(> -0.8\) but \(< +0.8\); and ID \(> +0.8\). The five species whose ID was \(> +0.8\), namely *A. chartifex sp., A. instabilis, C. limata, E. tuberculatum* and *W. aureopunctata* were all species which had already been classified as dominant by the three subjective criteria mentioned above (the dominants *C. erecta* and *C. acuta* were not found during the 1160-tree survey). Furthermore, the 56 species with ID values \(< -0.8\) were all species which, on the basis of the subjective criteria, would all be regarded as non-dominant species. A further 10 species occurred in the middle ID range. These were generally species which exhibited moderate density values but which did not monopolize large tracts of canopy. They did, however, exhibit a number of negative associations with other species, and we regard this group as sub-dominant species.

Figures 2 and 3, respectively, show the positive and negative associations between the ant species used in the aforementioned analysis. The diagrams show associations which are significant at the 5 percent and 10 percent levels, respectively, by solid and dotted lines, and the species considered to be dominant or sub-dominant are respectively shown boxed or in boldface. The dominant ants exhibit at least one negative association with another dominant ant. Furthermore, the 10 sub-dominant ants shown in Figure 1 also exhibit negative associations with at least one dominant ant. With just two exceptions (*Crematogaster sp., proox. limata with Paratrechina sp. 124, Camponotus abdominalis with Camponotus retusus*), negative associations between sub-dominant ants were not found. With the exception of the association between *E. tuberculatum* and *Pheidole sp. 103*, there are no significant positive associations between dominant and other ant species. There are, however, many positive associations between sub-dominants and non-dominants and between certain pairs of sub-dominant species. The overall result of this is for groupings of non-dominant ants to occur in association with certain sub-
dominant species (e.g., Camponotus cingulatus, Ca. abdominalis, Ca. crassus, Crematogaster curvispinosa, Monomorium floricola, and Paratrechina sp. 124), with a tendency for these groupings to meld together through the association between certain sub-dominant species (e.g., Ca. crassus and Paratrechina sp. 124).

ANT DISTRIBUTION.—Ninety-one species of ant were found on trees in the four plots where ants were mapped. Of these, 40, 43, 34, and 37 species were found, respectively, in Plots 1, 2, 3, and 4. The distribution of dominant ants and one sub-dominant ant in each plot is shown in Figure 4.

Ectatomma tuberculatum, which nests at the base of trees, was present on all but 12 cocoa trees in Plot 1 (Fig. 4a). The distribution range of this species was greater than this figure suggests; inspection of trees outside the plot indicated that it was present on many of the adjoining trees. The only other dominant in this plot was W. auropunctata. This species nests in leaf litter and wood cavities and, in this plot, usually occurred on the same trees with E. tuberculatum.

Three species of dominant ants were found in Plot 2 (Fig. 4b). Wasmannia auropunctata was distributed throughout most of the plot, except for the bottom-left of the area where A. instabilis was present. Crematogaster erecta was also widely distributed throughout the plot, often on trees which were occupied by one of the other two dominants.

Plot 3 supported five species of dominant ants (Fig. 4c). Both A. chartifex sparti and A. instabilis were present. The former species nests in large cavities constructed on trees and the latter nests in enclosed cavities such as hollow twigs or old cocoa pods. Wasmannia auropunctata occurred in the territory between these species and E. tuberculatum was the main dominant found in the bottom-right of the plot. Crematogaster erecta also occurred in this plot, often on trees where W. auropunctata or one of the two A. sparti spp. were present.

Plot 4, which comprised irregularly spaced, mature trees, supported three dominant Crematogaster spp. (Fig. 4d). However, the majority of trees in this plot lacked dominant ants. It is interesting to note that Ca. cingulatus, which has sub-nests in old, hollow cocoa pods and which we regard as sub-dominant rather than dominant, was widely distributed throughout the plot. This species was uncommon in Plots 1 and 2, although it was present on many trees in Plot 3.

The number of gaps, or lacunae, in the mosaic of dominant ants was generally low, with 10, 7, and 3 percent of trees lacking dominants in Plots 1, 2, and 3, respectively. However, Plot 4 exhibited a different pattern in which dominant ants were absent from 76 percent of trees.
Influence of Dominants on Number of Associated Species.—The mean number of ant species which were found within the territories of the five most widespread dominant ants are shown in Table 1. Chemical knock-down data demonstrated that both *A. chartaefex spiriti* and *E. tuberculatum* had less ant species associated with them than the other three species, but no significant differences were apparent between these two species or between any of the other three species (One-way Analysis of Variance, $P < 0.05$).

The mean number of associated species per tree was 5.9 and 4.4 for *A. chartaefex spiriti* and *E. tuberculatum*, respectively. There was a considerable range in the number of associated ant species and a tendency for trees on which either of the above-mentioned species occurred to support only one, or no, other species of ant. There were almost invariably other ant species associated with *W. aequanuntata* and *C. venosa*, and both species exhibited mean values of 7.8 associated ant species per tree. *Azteca instabilis* was associated with generally higher numbers of ant species on most trees where it was sampled and had a mean of 8.8 species of ants per tree. However, interpretation of the data for
this species is limited by the low number of trees on which it was sampled.

Relationship between dominant ant and size of associated species.—Figure 5a shows frequency distributions of lengths of all 91 ant species which were encountered during the mapping of Plots 1–4. Analysis of the size range of ant species which occurred within the territories of the five most widespread dominant ants indicated that there were disproportionately fewer ants from the smaller size ranges within A. chartifex spiritus territory ($\chi^2 = 6.85, 3$ df, $P < 0.1$) and that there were disproportionately fewer species from the larger size categories within the territory of E. tuberculatum ($\chi^2 = 9.03, 3$ df, $P < 0.05$). The size range of those ant species which occurred within the ranges of A. instabilis, Cr. acuta and W. auropunctata did not significantly differ from the size range distribution of the overall ant fauna.

The influence of dominant ants on the size range of associated ants is more dramatically illustrated if data for all trees are treated separately and then summed. In other words, the data are treated so that the cumulative influence of dominant ants on successive trees can be observed. The tendency for the small A. chartifex spiritus to exclude small ants and for the large E. tuberculatum to exclude large ants is clearly seen (Figs. 5b and 5e). The lack of impact of A. instabilis and W. auropunctata on ant size distribution is also once again illustrated (Figs. 5c and 5d) although it is of interest to note that within the territory of Cr. acuta, there are considerably fewer ants in its own size range (Fig. 5d).

**CONTRIBUTION OF ANTS TO INVERTEBRATE BIOMASS.**—The biomass of ants, other invertebrates, and the percentage contribution of ants to total invertebrate biomass is shown in Table 1. Ant biomass ranged from 1.21–2.10 g per 16 m², depending on the

| Table 1. Mean biomass values and mean ant species richness for 16 m² chemical knockdown samples of cocoa canopy occupied by five different dominant ants |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|
|                                | Azteca chartifex spiritus ($N = 10$) | Azteca instabilis ($N = 5$) | Crematogaster erecta ($N = 13$) | Ectatomma tuberculatum ($N = 9$) | Wasmannia auropunctata ($N = 6$) |
| Number of species of ants in territory of dominant | 5.9 | 8.8 | 7.8 | 4.4 | 7.8 |
| Ant biomass (g) | 0.37 | 0.25 | 0.34 | 0.22 | 0.55 |
| Biomass of other arthropods (g) | 1.83 | 2.10 | 2.06 | 1.96 | 1.21 |
| Contribution of ants to total biomass (%) | 16.8 | 10.6 | 14.2 | 10.1 | 31.3 |
dominant ant. The contribution of ants to total intervebrage biomass ranged from 10.1–31.3 percent.

DISCUSSION

The ant mosaic.—The results of our mapping within cocoa confirm Winder's (1978) and Lesnoy's (1978) findings that arboreal-foraging ants in this part of Brazil are distributed in a mosaic-like fashion. We observed seven species of dominant ants within the mosaics which we mapped, although we have also observed Azteca paranaensis and Dolichoderus atro-
labiatus as dominants in cocoa elsewhere at CEPLAC (Delabie, unpublished data). In addition to these, Lesnoy (1978) has observed a number of other species at CEPLAC which he considered to be dominants. We believe that some of the species listed by Lesnoy may be sub-dominant rather than dominant species. The quantitative method for detecting dominance produced results which agreed with the checklist of dominants which we produced using the subjective criteria. It now remains for the robustness of the technique to be evaluated in other areas of Brazil, on other types of vegetation and in other areas of the tropics where a different ant fauna is involved.

The species which we indicated by the quantitative method to be members of the sub-dominant category were all ones which were capable of reaching moderate densities, albeit on a more localized scale than the dominant species. Some of these species may attain these densities in areas where lacunae in the mosaic of dominants occur; this could explain the wide-spread distribution of Ca. abdominalis in Plot 4 (Fig. 4d). Others, such as Pheidole sp. 103 (Fig. 2), may be capable of existing within the territories of certain dominant species by means of some behavioural or structural adaptation. The tendency for the sub-dominants to be associated with several non-dominant species in part reflects their less aggressive nature. It may also result from the species within the groupings exhibiting similar food or habitat requirements, although our knowledge of the ecologies of these species is not yet sufficient to evaluate this possibility.

In the younger, sprayed cocoa plantations the mosaic is densely packed, with few unoccupied trees. Indeed, the 90–97 percent occupancy of trees by dominants is as high or higher than in plantations surveyed in Africa or Asia (see summary in Major & Carrier-Pesci 1991). At this stage we are unsure why the degree of occupancy by dominants was so much lower in the unsprayed Plot 4. This plot comprised larger trees growing under heavier top-shade. One possibility was that the degree of insolation was too low for many of the dominants to thrive in this area. The fact that Lesnoy (1978) found many dominants in rain forest does not invalidate this suggestion, since he surveyed the mosaic along a cleared edge of the forest. The presence of a densely packed mosaic in the darker interior of such forest remains to be confirmed, although our observations indicate that the forest interior is not as densely packed with dominant ants (Major & Delabie, unpublished data). A second possibility is that the mosaic may be a feature of an earlier part of the succession of the cocoa farm community. Thus, either the repeated spraying of the cocoa, or the young age of the trees may have favoured the presence of the ant species which comprise the mosaic. At this stage we have insufficient evidence to confirm or refute this suggestion. Finally, dominant ants may have been distributed on the shade trees above the cocoa canopy. Although we did not investigate this possibility, it may be that the mosaic in old cocoa or in forest is more horizontally segregated, with dominants tending to be distributed in the upper canopy strata.

The analysis of association between ant species confirms what has been observed elsewhere, that the dominant ants tend to exclude other dominants from within their territory. The existence of more than one dominant species on a tree, such as was observed in Plots 1 and 2 (Figs. 4a and 4b), may result from different species using different parts of the tree. This could certainly be the case for W. eupunctata, which tends to forage on the lower trunk of trees, and C. erecta which spends more time on the outer branches and foliage. Another possible reason for the apparent co-existence is that the boundaries between ant territories may occur within, rather than between, individual trees. This has certainly been observed on cocoa trees in Ghana (Major 1972) and, since the canopy of adjacent trees is largely continuous, could well be the case in the plots described here.

The analysis of the number, and length, of sub- and non-dominant ants associated with each dominant suggests that at least two of the species, A. chloritex sp. eti and E. tuberculatum, can exert a profound influence on both the number and length of ant species which occur within their territory. In the case of these two species, and possibly also of C. erecta, the ants most similar in size to the dominant were the ones which were excluded. We consider the alternative explanation, that dominants occurred on trees because similar sized ants were
FIGURE 4. Distribution of dominant ants on cocoa trees in (a) Plot 1, (b) Plot 2, (c) Plot 3, and (d) Plot 4 at CEPLAC, Isaboa. The distribution in Plot 4 of the sub-dominant, Camponotus singulatus is also shown. Shade trees are illustrated by dotted lines and each plot has been drawn twice so that the distribution of individual species may be shown more clearly. Key: O Azteca chartifera sp ritual; O A. insidiosus; O Camponotus singulatus; O Crematogaster acuta; O Cr. erecta; O Cr. limata; O Ectatomma tuberculatum O Wasmannia auropunctata.
FIGURE 4. Continued.
absent, to be most unlikely. In terms of reduction in the number of associated ant species, *A. chartifex spiriti* and *E. tuberculatum* appeared to exert the greatest impact. This suggests that, of the species investigated, these two species were the most strongly interactive ants.

If the number and size of ant species were influenced by the dominant ant, it is not surprising that species composition may also be influenced by the dominant. This is indeed the case, as certain non-dominants were either positively or negatively associated with particular dominants (Figs. 2 and 3). This tendency for non-dominants to be associated with dominant and sub-dominant ants has also
been noticed for Venezuelan cocoa by Jaffe, Tablante, and Sanchez (1986) and for Ghanaian cocoa by Room (1971).

The range in ant biomass of 0.22–0.55 g per sample (0.01–0.03 g m⁻²) indicates that ants comprise a sizeable component of invertebrate biomass in the cocoa (10.1–33.3% of total invertebrate biomass). Although the values were high, the percentage contribution of ants to invertebrate biomass for four of the five dominant ants (Table 1) is lower than the value of one-third cited by Fitikau and Klinge (1973) or 26–47 percent cited by Adis, Lubin, and Montgomery (1984) for Amazonian rain forest. By contrast, however, the abundance of ants in our cocoa plots was considerably higher than in coffee plantations at Viçosa, in the state of Minas Gerais, Brazil (Majer & Querez, in press), which is much further south than Bahia. Possibly there is a gradient of increasing arboreal ant abundance from the subtropical parts of Brazil through to the tropical regions.

The data reported in this paper are of interest because they show how ants contribute to the structuring of arboreal arthropod communities. The information presented also complements the qualitative observations described by Leston (1978), which were largely made in nearby rain forest. It would be informative if the dominance of ants in the local rain forest could also be investigated using the procedures which we have used in the present study. In addition to its inherent ecological interest, these findings are also relevant to the potential for using ants as biological control agents for tree crop pests. The beneficial aspects of ants in Brazilian cocoa has already been reviewed by Delisie (1990) and, in a companion paper to the present one, we investigate the potential of the ants mentioned in this paper as biological control agents.

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LITERATURE CITED


