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Ant Species in Tropical Australian Tree Crops and Native Ecosystems—Is There a Mosaic?¹

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ABSTRACT

Dominant arboreal ants are distributed in a mosaic-like fashion within tree-crop plantations throughout the New World and Old World tropics. This paper reports on the distribution of arboreal ants within mango plantations, rain forests, and woodlands in the tropical northern part of Australia. Only two genera of arboreal ants, *Oecophylla* and to a lesser extent *Crematogaster*, reach high densities on trees in the areas studied. Both genera tend to occupy large blocks of canopy, but in the spaces between their colonies the canopy is either devoid of ants, occupied by arboreal-nesting species of low colony size, or visited by ground-nesting species. The latter do not monopolise large, contiguous blocks of canopy. The result is a partial ant mosaic of *Oecophylla* and *Crematogaster* territories with few, or no, ants on the surrounding canopy.

The situation in tropical Australia is compared with published records from elsewhere in the world, and the reasons for the differences which exist are discussed. Finally, the implications for pest management in Australian tropical tree crops are speculated upon.

DOMINANT ARBOREAL ANT SPECIES THROUGHOUT the New and Old World tropics are distributed in a mosaic-like fashion within tree-crop plantations (see recent review by Jackson 1984a). The three-dimensional patchwork of non-overlapping dominant species is thought to arise from competitive interactions and also by their differing microhabitat selection profiles (Leston 1973). In view of the strong interactions which exist between these and the less numerous non-dominant species, the latter also form a mosaic which reflects the distribution of the dominant species with which they are able to co-exist (Room 1971).

Studies on the ant mosaic are of interest to theoretical ecology because of the information they provide on the competitive interactions between different species of ants (Jackson 1984b). Also, since dominant ants may influence the abundance and distribution of other taxa, their role in community organization (Gilbert 1980) and in moulding evolutionary processes (Wilson 1958) is of great interest. The existence of the mosaic also has practical implications because the dominant ants may dictate the distribution of certain pests or pathogens within the tree-crop. In a recent book concerning economically important social insects, Gotwald (1986) reviewed the beneficial economic role of ants in agroecosystems, and Majer (1986) discussed the way in which such ants could be selected and utilised in pest control programmes.

To date, ant mosaics have been described from various parts of Africa (see papers quoted in Jackson 1984a), from tropical Asia (*e.g.*, Greenslade 1971) and from Brazil (Leston 1978). Most of the observations have been performed in tree-crop plantations, although Leston's (1978) study was undertaken in rain forest, and Hölldobler (1979) mapped the distribution of *Oecophylla longinoda* in a Kenyan forest.

The northern extremity of Australia, which experiences a tropical monsoonal climate, is generally referred to as a semi-arid tropical region. Associated with this are patches of rain forest, also known as vine thicket forest, within a large expanse of sclerophyllous, *Eucalyptus*-dominated savanna. Much of the tropical monsoonal region remains under native vegetation, with only very small areas cleared for pastoral use or for tree crops such as mango or citrus. There is little published information on the arboreal ants in this part of Australia. Lokkers (1986) has described the distribution of *Oecophylla smaragdina* throughout northern Australia, while Hölldobler (1983) has mapped the distribution of this species in cleared forest in Queensland. Greenslade (1985) has highlighted the interaction of arboreal *O. smaragdina*, *Tapinoma* sp. 16, *Paratrechina* nesting ants in rain forest and *Eucalyptus* woodland in the Alligator Rivers region of the Northern Territory. More recently I (JDM) have provided quantitative data on the abundance and diversity of arboreal ants in rainforest and mango plantations in northern Australia and also in sclerophyll habitats of southern Australia (Majer 1990). The diversity

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of arboreal ants, both tree- and ground-nesting, was found to be low in Australian rain forests in comparison with elsewhere in the humid tropics, and it is often lower than that of the nearby *Eucalyptus* forest. Except where *O. smaragdina*, or perhaps *Crematogaster* spp., are present the trees of rainforests and plantations lack dominant ants. Potential reasons for the low diversity of, and degree of dominance by, arboreal ants in tropical monsoonal Australia are discussed in Majer (1990).

This paper extends my observations on the abundance and diversity of arboreal ants in northern Australia by asking the question: is there an ant mosaic in tree-crop plantations or native vegetation in this seasonal tropical region?

METHODS

STUDY SITES.—Studies were conducted at three locations in tropical northern Australia. The Kununurra (Western Australia) and Darwin (Northern Territory) sites were mango plantations, whereas the Mt Trafalgar (Western Australia) site was an area of rain forest adjoining a sclerophyllous woodland formation.

Kununurra, Department of Agriculture mango plantation.—This was a 1 ha plantation of 4-year-old trees planted on a 10 × 10 m spacing and, at the time of the survey, of 2–5 m in height. Glyphosate had been applied five times during the year for weed control and trichlorfon had been used infrequently for insect control.

Kununurra, Pederick's mango plantation.—This was a 0.9 ha area of 11-year-old trees planted on a 10 × 10 m spacing. Trees ranged from 7–9 m in height and the site had a 30–100 cm high shrub cover. Glyphosate had been applied four times per year to reduce weed growth, but no pesticides had been sprayed on the trees.

Kununurra, Wilford's mango plantation.—This 0.5 ha plantation contained 18-year-old trees planted on a 10 × 10 m spacing and reaching a height of 10–14 m (Fig. 1). The area had been treated with glyphosate three times throughout the year to reduce weed growth and chlorpyrifos had been sprayed prior to harvesting to reduce ant numbers.

Darwin, Brigden's mango plantation.—The trees of this 0.8 ha plantation were spaced at distances ranging from 5 to 10 m. The trees nearest the house

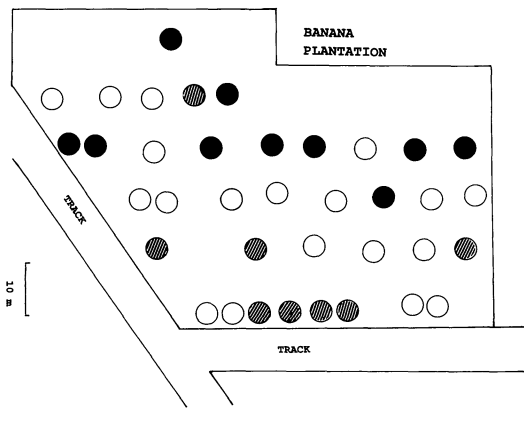


FIGURE 1. Distribution of mango trees (circles) during December 1986 in Wilford's mango plantation at Kununurra, Western Australia. The black and hatched circles indicate the presence of *Oecophylla smaragdina* and *Crematogaster* sp., respectively.

(Fig. 2) had been planted during 1974–5 while those at the far end of the property had been planted during 1982–3. Younger trees had also been planted in the gaps caused by death of older trees. Trees ranged from 2–10 m in height, depending on their age. No herbicides or pesticides had been applied to this plantation, and the shrub layer was about 120 cm tall.

Mt Trafalgar forest.—This was an interface between sclerophyll woodland dominated by *Eucalyptus* spp. and *Adensonia gregoria*, which ranged from 10–20 m in height, and a rainforest area of small trees, largely less than 25 cm trunk diameter and 6 m height (Fig. 3). The woodland trees and the large emergent trees in the rainforest were mapped by gridding the area out. The extremely numerous small rainforest trees were not mapped as they were too numerous.

SAMPLING

Sampling methods fell into five categories.

Mapping of arboreal ants.—The individual trees in Wilford's mango plantation, Brigden's mango plantation, and the Mt Trafalgar forest (except the small rainforest trees) were mapped in December 1986, December 1987 and July 1988, respectively. Each tree was inspected for a period of five minutes, and the ants which foraged on the trunk or leaves were collected for later identification. The canopy of tall trees was inspected with the aid of binoculars. The

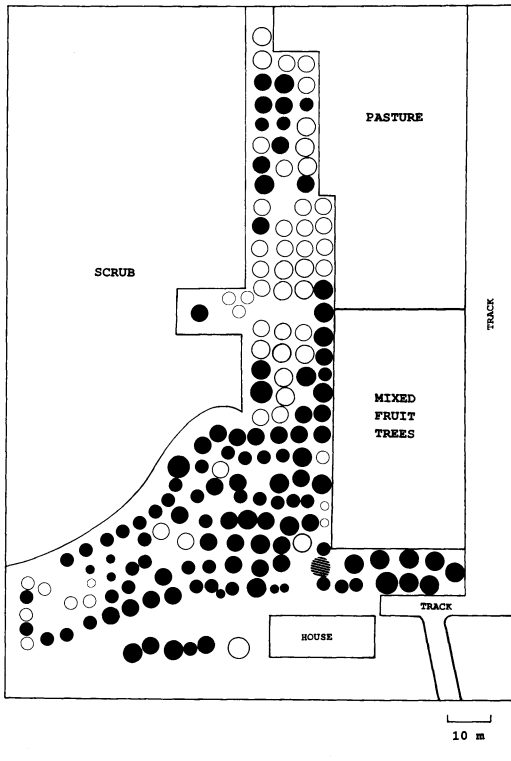


FIGURE 2. Distribution of mango trees (circles) during December 1987 in Brigiden's mango plantation at Darwin, Northern Territory. The black and hatched circles indicate the presence of *Oecophylla smaragdina* and *Crematogaster* sp., respectively.

nesting habit of each species was recorded and a subjective assessment of the general abundance of each species on trees was noted. If more than 200 ants could be seen on the tree and individuals were present on the trunk and on several branches, the ant was regarded as dominant.

Mapping of terrestrial ants.—The ground surface of Wilford's mango plantation was marked out on a 3×3 m grid and 2 cm diameter pitfall traps were sunk at each grid marker. Traps contained 20 ml of 70 percent ethanol plus 30 percent glycerol (v/v) and were left in the ground for 7 days during December 1986. The ants within the 254 traps were counted and identified.

Quantification of ants in trees.—Suitable areas of mango canopy were selected in January 1986 from within Wilford's mango plantation or from nearby areas containing large trees. The ant fauna was then sampled in five areas of mango canopy which were dominated by *O. smaragdina* and five which were

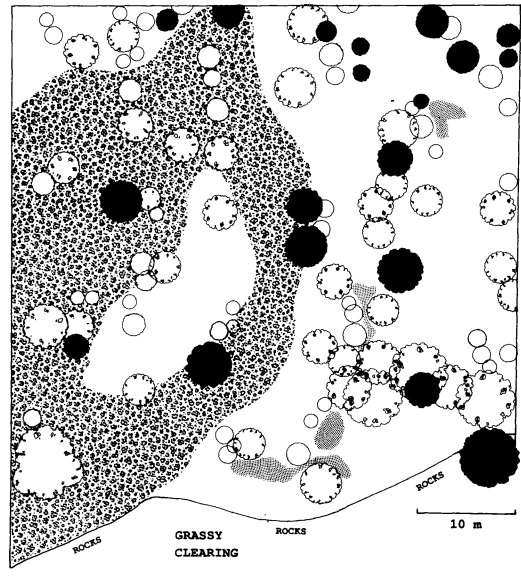


FIGURE 3. Map, prepared during July 1988, of interface between rainforest (left) and sclerophyll woodland (right) at Mt Trafalgar, Western Australia. The woodland trees and tall emergents in the rainforest are mapped, and the heavily stippled area shows the numerous small rainforest trees. The black trees are where *Oecophylla smaragdina* is present and the dotted stipple indicates areas of shrubs which are also occupied by this species. The distribution of *Crematogaster* sp. is not shown although it was present on some of the small rainforest trees.

not. Prior to sampling, the undergrowth was slashed in order to facilitate the placing of 25 m^2 squares of calico beneath the canopy. On the following day the canopy was sprayed with 0.5 percent synthetic pyrethrin using a two-stroke petrol mistblower with a vertical throw of about 10 m, which proved adequate to sample the trees. After 30 min the canopy was shaken to dislodge dead or dying animals and these were transferred from the sheets to vials of 70 percent alcohol. A similar method of sampling has been successfully used by Majer (1973, 1976a) in Ghanaian cocoa plantations. The animals were sorted and counted to order or family level and the specimens were then drained for 12 hr in filter paper funnels. The resulting weight of the sample was considered to be an estimate of live weight of the animals in the 0–10 m stratum.

Ant baiting experiments.—A baiting program was designed to determine whether the presence of *O. smaragdina* influences the other ant species present and also to assess which species, if any, were feeding on or monopolizing food resources in the trees and

on the ground. The baiting program was conducted in Wilford's mango plantation over a 24 hr period on 6 December 1986. It involved placing cracked wheat, diluted honey, and sardine in separate compartments of a petri dish. This method was designed by Greenslade (1985) and aims to attract seed feeding, nectar feeding, and predator/scavenger ant species respectively. Baiting stations, which consisted of one bait dish in the tree and one at the base, were placed on 10 *O. smaragdina*-dominated trees and on 10 trees where this species was absent.

Succession of arboreal ants.—The frequency of arboreal ants within the three Kununurra plantations was assessed by visiting each tree and recording the species which were present on the trunk or leaves. Each tree was inspected for a period of five minutes during January 1986 and observations were confined to the period from 5 to 9 am, when temperatures were less than 40°C. Ants were regarded as arboreal if they were foraging on the trees, even if their nests were on the ground.

RESULTS

Distribution of ants.—A total of 30 ant species was found in Wilford's plantation, of which 28 were present on the ground, 13 were present on the trees and 11 were common to both strata (Table 1). Six of the species present on trees are believed to nest on the trees or under dead wood on the lower trunk, five (*Iridomyrmex sanguineus*, *Iridomyrmex* sp. 13, *Paratrechina* sp. 11, *Camponotus* sp. 18, *Polyrbachis ammon* gp) nest in the ground but commonly forage on trees, *Iridomyrmex* sp. 8 and *Opisthopsis haddoni* gp nest in the soil but seemed to forage preferentially on trees, while other species are strictly epigaeic. The most frequently sampled ants on the 37 trees were observed on approximately 10 of the small *O. smaragdina*, *Tapinoma* sp. 16, *Paratrechina longicornis*, *Crematogaster* sp. 9 and *Iridomyrmex* sp. 8. Of these, only *O. smaragdina*, and to a much lesser extent *Crematogaster* sp. 9, occurred in large numbers on the trees. Ten of the 37 trees were occupied by *O. smaragdina* and a further eight by *Crematogaster* sp. 9 (Fig. 1); the two species never occurred on the same tree, and their distributions were negatively associated ($P < 0.05$, Fisher's test). There was a tendency for both species to occupy contiguous trees although the colony boundaries were not elucidated during this survey.

The four other widespread arboreal species are excluded from Figure 1 for reasons of clarity and also because they were not abundant. However, *O.*

'*haddoni*' was diffusely distributed throughout both the ground and trees, with a distribution which overlapped both *O. smaragdina* and *Crematogaster* sp. 9. Small isolated nests of *Tapinoma* sp. 16 were on trees scattered throughout the plot; *P. longicornis* was clumped on the ground and trees next to the banana plantation and was negatively correlated with *Crematogaster* sp. 9 ($P < 0.05$, Fisher's test); while *Iridomyrmex* sp. 18 was scattered throughout the plot. Apart from the cases outlined above, application of Fisher's test revealed no significant negative associations between any of the six most frequently occurring arboreal ant species.

At Brigden's mango plantation (Fig. 2) *O. smaragdina* occurred on 115 (67%) of the trees while *Crematogaster* sp. (apparently the same as at Kununurra) was present on only one tree. *Opisthopsis 'haddoni'* was present on four trees, two of which were also foraged by *O. smaragdina*. Of the remaining trees, a large trail of *Iridomyrmex* sp. ascended one tree, a few individuals of *Camponotus* sp. were present on two trees, and *Paratrechina* sp. was present on one tree. No ants were observed on 50 of the trees although it should be noted that these were generally the smaller, more recently planted trees.

The distribution of *O. smaragdina* in the rain forest and sclerophyll woodland at Mt Trafalgar is shown in Figure 3. Small trails of *Crematogaster* sp. were observed on approximately 10 of the small rainforest trees, but none of the large ones. No other species of ants were mapped during this survey although several species of *Polyrbachis* were observed on rainforest and woodland trees. With the exception of *O. smaragdina* and, to a lesser extent *Crematogaster* sp., no other ant species were abundant on the trees.

Oecophylla smaragdina was absent from almost all rainforest trees which, as a result of their high density, created an extremely shaded environment. This ant was present on four of the tall emergent trees in the rainforest and on 15 of the woodland trees. It was also present on a series of shrubs running diagonally through the woodland. The nature of the foraging trails indicated that the ants on the shrubs formed two separate colonies and that these were part of those present on nearby trees. Some of the trees appeared to support discrete colonies, whilst other colonies (e.g., top right corner of Fig. 3) occupied several trees.

Abundance of ants on trees.—The numbers of ants in the chemical knockdown samples, both within and outside *O. smaragdina* territory, are shown in

TABLE 1. Percentage frequency of ants in pitfall traps and on mango trees in Wilford's plantation, Kununurra, during December 1986. The nesting habit of each species is also shown.

| Subfamily | Genus and species | Nesting habit ^a | Percentage frequency | |
|-------------------------------|---|----------------------------|----------------------------|-------------------|
| | | | Pitfall traps (N = 254) | Trees (N = 37) |
| Ponerinae | <i>Rhytidoponera aurata</i> gp sp. 27 | G | 15.0 | — |
| Myrmicinae | <i>Cardiocondyla</i> sp. 23 | G | 3.1 | — |
| | <i>Monomorium</i> sp. 12 | G/D | 17.0 | — |
| | <i>Monomorium</i> sp. 17 | G | 67.7 | — |
| | <i>Monomorium</i> sp. 22 | G | 22.4 | — |
| | <i>Monomorium</i> sp. 30 | G | 51.0 | — |
| | <i>Monomorium</i> sp. 31 | T(?) | — | 2.9 |
| | <i>Monomorium</i> sp. 32 | G | 0.8 | — |
| | <i>Pheidole</i> sp. 28 | G | 12.2 | — |
| | <i>Pheidole</i> sp. 29 | G | 2.0 | — |
| | <i>Tetramorium</i> sp. 20 | G | 11.0 | — |
| | <i>Crematogaster</i> sp. 9 | T | 1.2 | 22.8 |
| | <i>Meranoplus</i> sp. 33 | G | 0.4 | — |
| | Dolichoderinae | <i>Tapinoma</i> sp. 16 | T | — |
| <i>Iridomyrmex sanguineus</i> | | G | 31.5 | 5.7 |
| <i>Iridomyrmex</i> sp. 5 | | G/D | 6.7 | 8.6 |
| <i>Iridomyrmex</i> sp. 7 | | G/D | 2.4 | — |
| <i>Iridomyrmex</i> sp. 8 | | G | 1.2 | 20.0 |
| <i>Iridomyrmex</i> sp. 13 | | G | 67.7 | 2.9 |
| Formicinae | <i>Paratrechina longicornis</i> | G/D | 16.1 | 25.7 |
| | <i>Paratrechina</i> sp. 11 | G | 4.3 | 5.7 |
| | <i>Camponotus</i> sp. 4 | G | 1.2 | — |
| | <i>Camponotus</i> sp. 18 | G | † | 2.9 |
| | <i>Camponotus</i> sp. 21 | G | 2.0 | — |
| | <i>Opisthopsis haddoni</i> gp sp. 1 | G | 3.9 | 82.9 |
| | <i>Polyrbachis ammon</i> gp sp. 6 | G | † | 2.9 |
| | <i>Melophorus aeneovirens</i> gp sp. 25 | G | 16.9 | — |
| | <i>Melophorus</i> sp. 24 | G | 44.9 | — |
| | <i>Melophorus</i> sp. 26 | G | 12.2 | — |
| <i>Oecophylla smaragdina</i> | T | 1.2 | 28.6 | |

^a G = ground, T = tree, D = dead wood on lower trunk of tree.

† Not present in pitfall traps but observed foraging on ground.

Table 2. With one exception, numbers of *O. smaragdina* were always higher than those of the most abundant ant in the other five knockdown samples (277–8883 per 25 m² sample). On average, *O. smaragdina* contributed 60 percent to the total wet weight of invertebrates.

The samples taken from outside *O. smaragdina* territories comprised a range of ant species. Numbers of *Iridomyrmex* sp. 5 were fairly high (424) in one sample although this was caused by the knockdown position coinciding with a nest in some dead wood on the trunk of the tree. The other knockdowns, which were characterised by *Crematogaster* sp. 9, *Iridomyrmex* sp. 8 and *O. 'haddoni'*, all produced low numbers of ants, contributing between 6.2–15.0 percent of total invertebrate biomass.

Interaction between terrestrial and arboreal ants.—Nine species were observed at the ground baits while

12 came to baits on trees in Wilford's plantation. Eight ground-nesting species fed at ground baits, although *P. longicornis*, which nests on the ground and on dead wood of the lower trunk (Table 1), was also found on ground baits. Ants at tree baits (Table 3) included two tree-nesting species (*O. smaragdina* and *Crematogaster* sp. 9), two ground- or lower trunk-nesting species (*Monomorium* sp. 12 and *P. longicornis*), and a further eight ground-nesting species.

Table 3 also shows the number of individual feeding observations made at 10 baits situated both within and outside *O. smaragdina* territory. The presence of *O. smaragdina* appeared to have little impact on the number of species visiting baits or on the number of baits visited. The records of individual species were insufficient to tell if any of them were influenced by the presence of *O. smaragdina* although *Crematogaster* sp. 9 was only found

TABLE 2. Biomass of invertebrate samples, number of ants sampled, and percentage contribution of ants to total biomass from 25 m² areas of Kununurra mango canopy sampled by pyrethrin knockdown sampling during January 1986.

| Sample no. | Most abundant ant | Number of ants | Wet weight of sample (g) | | Percentage contribution of ants to biomass |
|--------------------|-------------------------------------|----------------|--------------------------|---------------------|--|
| | | | Ants | Other invertebrates | |
| 1 | <i>Oecophylla smaragdina</i> | 277 | 1.10 | 4.20 | 20.8 |
| 3 | <i>Oecophylla smaragdina</i> | 252 | 0.93 | 1.59 | 36.9 |
| 5 | <i>Oecophylla smaragdina</i> | 353 | 1.56 | 1.26 | 55.3 |
| 7 | <i>Oecophylla smaragdina</i> | 8883 | 37.79 | 1.77 | 95.5 |
| 9 | <i>Oecophylla smaragdina</i> | 6463 | 33.43 | 3.20 | 91.3 |
| Mean values | | 3246 | 14.96 | 2.40 | 60.0 |
| 6 | <i>Crematogaster</i> sp. 9 | 151 | 0.26 | 2.55 | 9.3 |
| 8 | <i>Crematogaster</i> sp. 9 | 182 | 0.18 | 1.02 | 15.0 |
| 2 | <i>Iridomyrmex</i> sp. 5 | 424 | 1.80 | 4.06 | 30.7 |
| 4 | <i>Iridomyrmex</i> sp. 8 | 30 | 0.13 | 1.35 | 8.8 |
| 10 | <i>Opisthopsis haddoni</i> gp sp. 1 | 135 | 0.17 | 2.56 | 6.2 |
| Mean values | | 184 | 0.51 | 2.31 | 14.0 |
| Cocoa ^a | <i>Oecophylla longinoda</i> | 4407 | 35.30 | 14.70 | 70.6 |
| | <i>Crematogaster striatula</i> | 3420 | 2.10 | 15.00 | 12.3 |

^a Data from Majer (1976b).

at baits situated outside the territory of the former species, which is consistent with previous observations (Fig. 1).

Succession of arboreal ants.—The percentage of trees in which ants foraged or nested in the 4-, 11-, and 18-year-old mango plantations are shown in Table 4. There was a progressive development in the diversity of species as the plantation age increased. Four of the species observed in the 18-year-old plantation during December 1986 were not observed during this particular survey, which was performed 11 months earlier. Three of these were infrequently found on trees in December (*Monomorium* sp. 31, *Iridomyrmex* sp. 13, and *Camponotus* sp. 18) and could have been missing during the January survey, while the slightly more common *Iridomyrmex* sp. 5 may have been influenced by seasonal factors during the January survey.

The tree-nesting *Crematogaster* sp. 9 was present in all three plantations although it became more frequent in older plantations. *Tapinoma* sp. 16, which also nests in trees, was present in the two older plantations while *O. smaragdina* was only present in the 18-year-old plantation. Most of the other species on trees in the young plantations were ground-nesting species, although *Iridomyrmex* sp. 7 and *P. longicornis*, which both nested on ground and lower trunks, were respectively present in the 11- and 18-year-old plantations.

DISCUSSION

The two surveys in mango plantations (Figs. 1 and 2) revealed a distribution of arboreal ants which is markedly different from that reported elsewhere for plantations in the humid tropics and which is consistent with the observations made in Queensland by Hölldobler (1983). There are only two dominant arboreal taxa in the Australian plantations, *O. smaragdina* and *Crematogaster* spp. (it is not known how many *Crematogaster* spp. from throughout northern Australia are involved at this stage). This contrasts with six dominant arboreal species in a Ghanaian cocoa farm (Majer 1972), at least seven species in Nigerian cocoa (Taylor 1977), five species in Cameroonian cocoa (Jackson 1984a), four species in Tanzanian coconuts (Way 1953), and four species in Solomon Islands coconuts (Greenslade 1971).

Further, of the two ant taxa which were observed to dominate the mango canopy, only *O. smaragdina* reached the abundance and biomass levels which are characteristic of arboreal ants in other tropical areas. For the purpose of comparison, data for the abundance and percentage contribution to total invertebrate biomass are given for *O. longinoda* and *Crematogaster striatula* in Ghanaian cocoa (Table 2). The values for *Oecophylla* spp. in Australia and Ghana are comparable, but the figures for *Crematogaster* spp. are considerably less in Australia than in Ghana. Thus, apart from the fact that

TABLE 3. Total number of ant feeding observations and total baits visited at arboreal baits placed within and outside *Oecophylla smaragdina* territory over a 24 hr period in December 1986. The number of occurrences at baits exceeds 10 because cumulative data for nine three-hourly observations are given.

| Ant species | Number of occurrences at baits where | |
|-------------------------------------|--------------------------------------|--------------------------|
| | <i>Oecophylla</i> present | <i>Oecophylla</i> absent |
| <i>Monomorium</i> sp. 12 | — | 1 |
| <i>Monomorium</i> sp. 17 | 2 | — |
| <i>Monomorium</i> sp. 22 | 1 | — |
| <i>Monomorium</i> sp. 30 | 1 | — |
| <i>Crematogaster</i> sp. 9 | — | 5 |
| <i>Iridomyrmex sanguineus</i> | 3 | 1 |
| <i>Iridomyrmex</i> sp. 8 | 1 | 2 |
| <i>Iridomyrmex</i> sp. 13 | 4 | 9 |
| <i>Paratrechina longicornis</i> | 2 | — |
| <i>Paratrechina</i> sp. 11 | — | 1 |
| <i>Opisthopsis haddoni</i> gp sp. 1 | 2 | 1 |
| <i>Oecophylla smaragdina</i> | 5 | — |
| Total ant occurrences | 21 | 20 |
| Number of species | 9 | 7 |
| Total baits visited (max = 10) | 8 | 7 |

they occupy territory on a range of contiguous trees, it is arguable whether Australian *Crematogaster* spp. can be considered dominant ants in the same way as congenetics elsewhere on trees of the tropics.

Data on ant mosaics elsewhere in the tropics have indicated that the majority of trees are used for foraging or nesting by dominant ants. For instance, maps of ants in Ghanaian cocoa trees have shown 70 percent occupancy by dominant ants (Majer 1976b), while similar data for Nigerian cocoa indicate 67 percent occupancy (Taylor 1977), for Cameroonian cocoa 69–79 percent occupancy (Jackson 1984a), for Tanzanian cocoa up to 100 percent occupancy (Way 1953), and for Solomon Islands coconut 78 percent occupancy (Greenslade 1971). The corresponding values for Wilford's Kununurra and Brigden's Darwin mango plantations are respectively 52 and 71 percent. The former value is a little lower than that noted at other tropical locations although the Darwin figure falls within the range reported elsewhere. It is possible that the low Kununurra figure is related to the spraying of insecticides some two months prior to the survey. However, observations on nearby unsprayed trees suggest that this occupancy rate is typical of even unsprayed trees. A more likely explanation relates to the fact that at Kununurra, *O. smaragdina* is on the southernly limit of its range. In moister areas, such as Darwin (mean annual rainfall = 1594 mm), the mosaic may be as densely packed as it is else-

TABLE 4. Percentage of trees foraged or nested by ants in 4-, 11-, and 18-year-old mango plantations at Kununurra during January 1986.

| | Name of plantation | | |
|-------------------------------------|--------------------|------------|-----------|
| | Dept. of Agric. | Pederick's | Wilford's |
| Age of plantation (yr) | 4 | 11 | 18 |
| Number of trees | 92 | 77 | 59 |
| Mean tree height (m) | 3.5 | 8 | 12 |
| Percentage of trees occupied by: | | | |
| <i>Opisthopsis haddoni</i> gp sp. 1 | 6.5 | 49.3 | 83.0 |
| <i>Crematogaster</i> sp. 9 | 6.5 | 1.3 | 11.9 |
| <i>Iridomyrmex sanguineus</i> | 9.8 | 7.4 | 6.8 |
| <i>Iridomyrmex</i> sp. 13 | 2.2 | — | — |
| <i>Polyrbachis ammon</i> gp sp. 6 | — | 6.5 | 6.8 |
| <i>Tapinoma</i> sp. 16 | — | 49.3 | >50.0 |
| <i>Iridomyrmex</i> sp. 7 | — | 5.2 | — |
| <i>Iridomyrmex glaber</i> gp sp. 15 | — | 11.7 | — |
| <i>Camponotus</i> sp. 18 | — | 9.1 | — |
| <i>Oecophylla smaragdina</i> | — | — | 23.7 |
| <i>Iridomyrmex</i> sp. 8 | — | — | 72.9 |
| <i>Paratrechina</i> sp. 11 | — | — | 13.6 |
| <i>Paratrechina longicornis</i> | — | — | 6.8 |
| Total species | 4 | 8 | 9 |
| Percentage trees with ants | 23 | 71 | 97 |

where in the tropics although, as already mentioned, it consists of fewer dominant species.

Greenslade (1985) has already observed that *O. smaragdina* and *Crematogaster* sp. are the major species found on trees in rain forest near Darwin. The data on ant distribution in the rainforest/sclerophyll woodland interface (Fig. 3) suggest that the observations in plantations also apply to native vegetation. However, the fact that *O. smaragdina* was only found on the woodland and emergent rain forest trees suggests that this species is restricted by the dense shade of the more tightly packed understorey trees in the rain forest. This limitation on the distribution of *Oecophylla* has also been observed in West Africa where *O. longinoda* has a marked preference for highly insolated trees (Majer 1976c).

The baiting experiment suggests that there is a strong vertical stratification of tree-nesting ants; the two major tree-nesting species attended the tree baits, in this study, but were never seen at ground baits. This is not the case for the ground-nesting species which readily moved up trees to feed on baits, even where *O. smaragdina* was present and abundant. The inability of *O. smaragdina* and *Crematogaster* sp. 9 to monopolise ground baits highlights the ecologically important role which the ground ant fauna plays. Under certain circumstances the ground fauna clearly exhibits competitive superiority over those species which normally feed in the trees. *Oecophylla smaragdina* has been observed at ground-baits near Darwin (A. Andersen, pers. comm.). It would, therefore, be interesting to repeat the experiment at Darwin, where conditions appear to be more favourable to *O. smaragdina*, to see if this species exerts a greater influence there.

Mango plantations, rain forests, and the denser sclerophyll woodlands of parts of northern Australia, therefore support a simplified ant mosaic consisting of two genera of ants, only one of which reaches true numerically dominant status. Why is the arboreal mosaic so simplified when compared with other tropical parts of the world? Majer (1990) has already speculated upon the paucity of arboreal ants in northern Australia, and the possible reasons which were advanced include the strongly seasonal climate

of the area or the productivity of the rainforest may limit the abundance of ants, arboreal ants may be limited by competition from ground-dwelling ants, or there may be some biogeographic explanations.

The results of the baiting experiment and those from Greenslade's (1985) survey of ants in forests and woodlands near Darwin certainly lend support to the second explanation. However, for the reasons advanced by Majer (1990) it is possible that all of these factors may play some part in producing a mosaic of the simplicity which has been observed in this study.

The data on ants in plantations of different age (Table 4) indicate a succession of ants, which has probably not reached a climax stage by the stage of the 18-year-old plantation. The succession is characterised by a gradually increasing richness of the ant fauna and by a gradual acquisition of arboreal-nesting species. The fact that *O. smaragdina* does not colonise trees until some time between 11 and 18 years may have economic implications. Mangoes in Australia are subjected to a range of pest species including millipedes (Diplopoda), red-banded thrips (*Solenothrips rubrocinctus*), mango scale (*Pbenacaspis dilatata*), and the red and black leafhopper (*Eoscarta* sp.). Although it was not the purpose of this study to find out, it is possible that *O. smaragdina*, and possibly *Crematogaster* spp., have some limiting effect on these pests. If this were found to be the case, it may be possible to utilize an integrated control scheme which incorporates the limiting effect of one or both of the ant genera which comprise the partial ant mosaic of northern Australian tree crops.

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