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The Abundance and Diversity of Arboreal Ants in Northern Australia[1]

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ABSTRACT

This paper collates survey data on the abundance and diversity of arboreal ants in subtropical and tropical rain forests in northern Australia. Data on arboreal ants in nearby *Eucalyptus* forests and also from *Eucalyptus* vegetation in southwest Australia are presented for comparison. The diversity of arboreal ants, both tree- and ground-nesting, is low in Australian rain forests in comparison with other tropical regions and it is sometimes lower than that of nearby *Eucalyptus* forest. Except where *Oecophylla smaragdina,* or perhaps certain *Crematogaster* spp. are present, the trees of the tropical and subtropical rain forests lack dominant ants. Reasons for the low diversity of, and degree of dominance by arboreal ants in Australian rain forests are speculated upon. Reasons include the possibility that the role of ants has been replaced by some other taxon; the strong seasonal climate or the productivity of such forests may limit the abundance of ants; arboreal ants may be limited by competition from ground-dwelling ants; or, alternatively, there may be some biogeographic explanation.

THROUGHOUT THE TROPICS, ANTS have been reported as comprising a major component of rain forest canopies and of the canopies of tropical tree crops. Examples of such observations include those of Fittkau and Klinge (1973), Leston (1978), Erwin (1983) and Adis *et al.* (1984) for Brazil; Erivin (1985) and Wilson (1987) for Peru; Room (1971) and Leston (1973) for Ghana, West Africa; Way (1954a, b) for Tanzania, East Africa; and Stork (1987) for Borneo. The data of Way (1954a, b), Room (1971) and some of those of Leston (1973) are from coconut and cocoa plantations, although these are believed to represent a similar situation to that in rain forest canopy. Observations in rain forests close to the plantations suggest that ants are also abundant in the canopy there.

Fittkau and Klinge (1973) estimated that ants constitute nearly a third of the arboreal arthropod biomass in Brazilian rain forest and this figure was confirmed by Adis *et al.* (1984) (29 percent of total arthropod biomass, or 51 percent of total numbers). Leston (1973), quoting data of Majer (1973), indicated that the Ghanaian cocoa fauna consisted on average of 89 percent ant individuals while in Borneo, Stork (1987) showed that ants comprised 18 percent of individuals in the arthropod tree fauna. The diversity of arboreal ants in the tropics also tends to be high. For instance, Room (1971) sampled 35 species of ants from 250 m^2 of cocoa canopy in Ghana, Wilson (1959) found 56 species of ants in approximately five km^2 of New Guinea rain forest canopy, while Wilson (1987) found 135 species in the canopy of a comparable area of Peruvian Amazon rain forest. Of the ants found within the canopy, a few species tend to predominate. Based on observations in West Africa, Leston (1973) nominated these species as dominant ants because of their numerical superiority and their tendency to exclude other dominant species from their territory. This dominance of a diverse, arboreal ant fauna by a relatively low number of species has also been noted in South America (*e.g.,* Leston 1973, Wilson 1987) and in Asia (*e.g.,* N. E. Stork, pers. comm.). The existence of these mutually exclusive dominant ants has tended to result in a mosaic of dominant species (Leston 1973), which then influences the distribution of non-dominant species (Room 1971).

There is some information, much of it unpublished, on the abundance of arboreal ants in southern Australia. Woinarski and Cullen (1984) found that ant individuals made up less than 2 percent of the arboreal arthropod fauna in forests and woodlands throughout the southern state of Victoria. By contrast, Yen (in press) found that ants made up 43 percent of arthropod individuals on Victorian mallee trees (a low-growing assemblage of *Eucalyptus* spp.). By drawing on Greenslade's (1979) description of an ideal Australian ant habitat, Yen attributed the high abundance of ants in this region to the mallee providing an optimal habitat for ants. Specifically, the mallee provides a mosaic of bare ground (which permits insolation of soil, unimpeded foraging, and provides ground for next excavation), litter (which provides shelter) and plants (which provide prey,

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TABLE 1. *Descriptions of the vegetation and climate of study sites. Field observations were made at all sites, while at some, qualitative information was obtained by sticky trap transect sampling (1) or by chemical knockdown sampling (2).*

Study area	Vegetation surveyed	Climate type and mean annual rainfall[1]
Karragullen, W.A. (1, 2)	Tall, open *Eucalyptus marginata* forest	Mediterranean (1069 mm)
Dryandra, W.A. (2)	*E. wandoo* woodland	Mediterranean (507 mm)
Kununurra, W.A. (2)	Mango plantation	Tropical monsoonal (813 mm)
Darwin, N.T.	Mango plantation	Tropical monsoonal (1594 mm)
Darwin, N.T. (1)	Monsoon forest	Tropical monsoonal (1594 mm)
Darwin, N.T. (1)	Tall, open *E. tetrodonta* forest	Tropical monsoonal (1594 mm)
Gove, N.T.	Tall, open *E. tetrodonta* forest	Tropical monsoonal (1362 mm)
Groote Eylandt, N.T.	Tall, open *E. tetrodonta* forest	Tropical monsoonal (1277 mm)
Weipa, Qld	Tall, open *E. tetrodonta* forest	Tropical monsoonal (1985 mm)
Kuranda, Qld	Complex mesophyll vine forest	Tropical monsoonal (2001 mm)
Mt Glorious, Qld (1, 2)	Complex mesophyll vine forest	Sub-tropical (1788 mm)
Mt Nebo, Qld (1)	Mixed *Eucalyptus* spp. tall, open forest	Sub-tropical (1788 mm)
O'Reilly's Guest House, Qld (1)	Mixed *Eucalyptus* spp. tall, open forest	Sub-tropical (1551 mm)
O'Reilly's Guest House, Qld (1)	Complex mesophyll vine forest	Sub-tropical (1551 mm)
Brisbane, Qld	Mixed *Eucalyptus* spp. tall, open forest	Sub-tropical (1253 mm)

[1] Rainfall taken from the nearest official recording station (Bureau of Meteorology, 1975).

nectar, and seed resources). Observations made by myself and other ant ecologists throughout Australia indicate that the use of trees in southern Australia by tree- or ground-nesting ants is generally not high, although ants are locally abundant on trees where conditions are optimal.

The only published information on the abundance of arboreal ants in tropical and subtropical regions of Australia is Lokkers (1986) who described the distribution of the "weaver ant," *Oecophylla smaragdina,* in northern Australia, and Greenslade (1985) who highlighted the interaction of arboreal *O. smaragdina* and *Crematogaster* spp. with ground-nesting ants in monsoon forest and *Eucalyptus*-dominated vegetation.

In this paper I collate my observations, gathered over the past eight years, on the composition of arboreal ant communities throughout the tropical and subtropical regions of Australia. The observations which I describe are presented in order to characterize the arboreal ant fauna of rain forests and tropical crop plantations. However, some *Eucalyptus* forest data from southern Australia and from areas adjacent to the rain forest plots are also described in order to provide a bench mark for comparison with the rain forest. Although the data were compiled from various independent projects, they are sufficiently standardized to enable comparisons to be made between various vegetation associations both within and outside Australia.

MATERIALS AND METHODS

Australia possesses a tropical monsoonal climate along its northern extremity and a subtropical climate along the upper reaches of the eastern seaboard. Associated with this are patches of rain forest of varying size, interspersed with sclerophyllous, *Eucalyptus*-dominated, vegetation. The forests and woodlands to the south, which experience a more temperate climate, are mostly dominated by various types of *Eucalyptus* species.

The study sites are listed in Table 1 and their location is mapped in Figure 1. Four of the sites are within the subtropical climatic zone, six are in the tropical monsoon region and two are situated in a southwestern Australian mediterranean zone. The latter have been included here in order to compare the tropical and subtropical ant communities with those from the south of the Continent. The vegetation types of each study site are also listed in Table 1.

The rain forest sites were either classified as mesophyll vine forest or, further north, as monsoon forest. The Kununurra, and one of the Darwin sites, were mango plantations. The remaining sites were vegetated with sclerophyllous *Eucalyptus* associations.

Sampling methods fell into three categories and some were only performed at certain sites (Table 1).

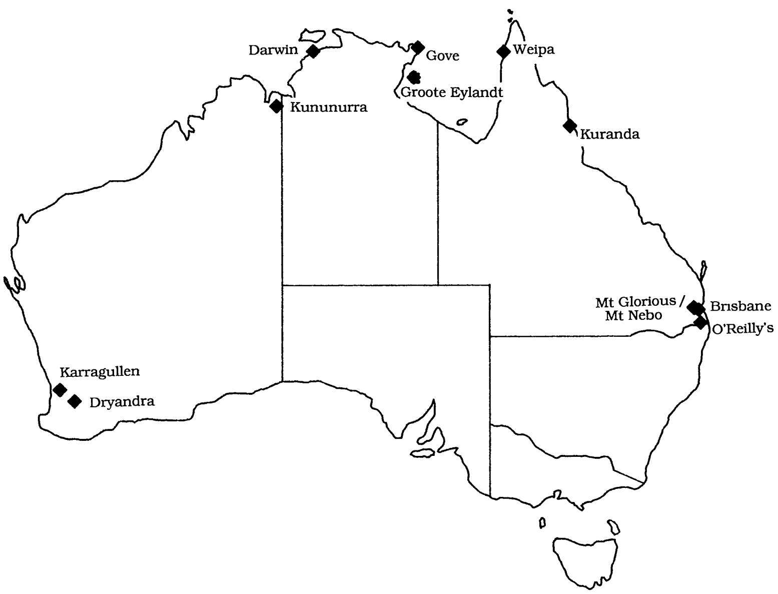

FIGURE 1. Distribution of localities where arboreal ants have either been sampled or where casual observations have been made.

STICKY TRAP TRANSECTS.—A band of 2.5 cm plastic tape was tied at a height of two m around the trunk of all trees along a 70 × 5 m transect. The tape was stapled to the trunk to ensure a tight fit, thus ensuring that all ants which traversed this part of the trunk had to cross this band. The band was coated with a sticky resin in order to trap the ants. The observations were designed to compare the abundance of arboreal ants in *Eucalyptus* forest vs mesophyll vine or monsoon forest. Ants were removed from the sticky band after one week, identified and counted. The Darwin sticky trapping study was performed by Paul Munns (1983) under the direction of Sylvia Lewis and myself. An identical procedure was used except that the ants on the sticky bands were accumulated over a six month period.

CHEMICAL KNOCKDOWN.—A suitable area of canopy was selected for sampling. Prior to sampling the undergrowth was slashed in order to facilitate the placing of sheets. A 25 m^2 square, or rectangle, of calico sheet was then placed 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. After 30 minutes the canopy was shaken to dislodge dead or dying animals and these were transferred from the sheets to vials of 70 percent alcohol. 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 approximate the live weight of the animals in the 0–10 m stratum. Although the vertical throw of the mistblower was adequate to sample the plantations, it did not reach the upper canopy of the rain forest which ranged from 20–50 m in height. Consequently the upper canopy was inspected with the aid of binoculars to verify if ant abundance was similar to that in the lower parts of the canopy.

The same method of sampling was used by Majer (1973, 1976) in Ghanaian cocoa plantations except that natural pyrethrum pesticide was used in that study. Some Ghanaian data are provided in this paper for comparison.

FIELD OBSERVATIONS.—These consisted of observing the canopy and trunks of trees of the relevant forests and woodlands for periods of time ranging from one day to one week, with at least some of the observations being performed at night. A subjective assessment of arboreal ant abundance was made and the species were identified.

RESULTS

The results of the sticky trap transect sampling are presented first. Table 2 shows the total ant species

TABLE 2. *Taxonomic breakdown of ant species obtained by sticky trap transect sampling on tree trunks in sclerophyll (S.F.) and rain forest (R.F.) throughout Australia.*

		Karragullen, W.A.	O'Reilly's, Qld	O'Reilly's, Qld	Mt Nebo, Qld	Mt Glorious, Qld	Darwin, N.T.	Darwin, N.T.
		S.F.	S.F.	R.F.	S.F.	R.F.	S.F.	R.F.
Myrmeciinae	*Myrmecia*		1					
Ponerinae	*Platythyrea*		1					
	Odontomachus						1	
Pseudomyrmecinae	*Tetraponera*							1
Myrmicinae	gen. nr. *Podomyrma*		1			1		
	Monomorium							1
	Chelaner		2					
	Crematogaster		1	1	2	1	3	2
Dolichoderinae	*Leptomyrmex*			1		1		
	Dolichoderus				1			1
	Iridomyrmex	1	4	1	2	1		
	Technomyrmex		1					
Formicinae	*Oecophylla*						1	1
	Myrmecorhynchus		1	1	1	3		
	Notoncus		1					
	Prolasius			1		1		
	Stigmacros			1				
	gen. nr. *Stigmacros*					1		
	Paratrechina							1
	Opisthopsis				1		1	1
	Camponotus	2	6	2	4	1	1	4
	Polyrhachis		3	1	1		1	2
	gen. indet.			1				
Total species per transect		3	22	10	12	10	8	14
Mean species per tree		0.5	2.7	0.4	2.6	1.0	3.1	5.8
Mean individuals per tree		3.6	6.3	0.4	9.1	2.4	ND[1]	ND[1]
Percentage of trees with ants		38	89	34	82	65	100	100

[1] ND = Data not given due to different length of sampling period used at Darwin.

per transect, the mean ant species per tree, the mean ant individuals per tree, and the percentage of trees with ants. It also gives a generic breakdown of the ants which were sampled.

The low diversity, abundance, and occupancy of trees by ants at Karragullen in southwestern Australia is clearly shown. Only *Iridomyrmex* sp. and two *Camponotus* spp. were collected from trees and 62 percent of trees had no ants on the trunk.

In subtropical Queensland the diversity, abundance, and occupancy of sclerophyll forest trees was considerably higher than that of southern Australia. The total species per transect and mean species per tree ranged from 12–22 and 2.6–2.7 respectively, and ant abundance on trees was between 2–4 times higher than in the south; the majority of trees had ants on the trunks. The fauna largely consisted of species of *Camponotus, Iridomyrmex, Polyrhachis,* and *Crematogaster,* although representatives from 13 other genera were also recorded. By contrast, the Queensland vine forest trees had fewer species (10 species per transect and 0.4–1.0 species per tree), considerably fewer individuals on their trunks and only 34–65 percent of trees had ants on their trunks (Table 2). The fauna consisted of species of *Myrmecorhynchus, Camponotus, Prolasius, Leptomyrmex, Iridomyrmex, Crematogaster,* and representatives from five other genera.

In Darwin the monsoon forest trees were occupied by a greater number of species than vine forest trees in southern Queensland (Table 2). Data on number of ant individuals are not given in view of the different sampling periods used for these trees. All trees were occupied by ants, which were mostly *O. smaragdina, Crematogaster* spp., *Camponotus* spp., and *Polyrhachis* spp. In contrast to the Queensland study, the diversity of ants in the monsoon forest exceeded that of the paired sclerophyll forest site. This may be associated with the exceptionally high abundance of *O. smaragdina* on the sclerophyll forest trees; competition from this aggressive ant is known to reduce the diversity of the associated ant community (Majer 1976).

Table 3 shows the results of the chemical knockdown samples, along with some data from Ghanaian cocoa which are described in Majer (1976). In the cocoa plantations, the abundance of the dominant cocoa ants ranged from 1236–4407 per 25 m^2 sample, depending on which ant species was involved. Put in terms of biomass, this ranged from 1.2–35.3 g wet weight of ants, or 5–72 percent of total arthropod biomass.

The southwestern Australian sclerophyll vegetation (mean canopy height 10 m) samples contained between 53–100 ants per sample, representing 0.2–0.4 g wet weight. The contribution of ants to arthropod biomass ranged from 6–12 percent although it should be noted that total arthropod biomass was low (3.2 g per 25 m^2 sample). Despite its more lush appearance, and the slightly higher total arthropod biomass, the mesophyll vine forest samples in Queensland produced a similar abundance and biomass of ants to that of the more southern samples (Table 3). The vine forest figures would have been higher had the entire canopy been sampled. However, the data are comparable with that of the southwestern vegetation since the height-range of canopy sampled was similar to that of the sclerophyll vegetation. Visual observations of the upper vine forest canopy indicated that ant abundance was similar to that of the lower canopy.

The mango plantation at Kununurra was partly colonized by *O. smaragdina.* These were distributed in large contiguous blocks of trees, between which there occurred *Crematogaster* sp., and a range of non-dominant *Iridomyrmex* spp., *Opisthopsis* sp., and other genera (J. D. Majer, pers. comm.). Consequently, the knockdown samples were stratified into two sets, one within, and one outside *O. smaragdina* territory. The results for both data sets are given. Outside the *O. smaragdina* territory, where there was no dominant species, the abundance of ants was only slightly higher than that in southern Australia or southern Queensland. The *O. smaragdina* samples contained 3245 dominant ants, comprising 86 percent of total arthropod biomass. The figures for *O. smaragdina* samples were closely in line with those for *Oecophylla longinoda* on cocoa in Ghana.

Extensive field observations by myself and other formicologists on trees throughout southern Australia, and at the sites shown in Figure 1, confirm the results of the sticky trapping and chemical knockdown sampling. Trees in sclerophyllous vegetation of many southern Australian sites lack dominant arboreal ants and close inspection reveals that they often have few or no ants on their trunks or foliage. Species which are found on southern trees include tree-nesting *Crematogaster* spp. or *Podomyrma* spp., although the majority of ants found on trees are ground-nesting *Iridomyrmex* or *Camponotus* spp.

In much of the tropical monsoon areas, the forests and plantations are partly dominated by *O. smaragdina.* Direct observations, and inspection of the chemical knockdown data in Table 3, indicates that this species is functioning as a dominant ant, reaching numerical dominance over other ant species and holding large blocks of territory. The only other

TABLE 3. *Abundance and biomass of ants in 25 m^2 chemical knockdown samples from tree canopies from various parts of Australia and from Ghana.*

Locality	Vegetation sampled	Dominant ant	Number of samples	Abundance of ants (x ± SD)	Total arthropod biomass (g) (x ± SD)	Biomass of ants (g) (x ± SD)	Percentage contrib. of ants to total arthropod biomass
Dryandra, W.A.	Wandoo woodland	No dominant	5	100 ± 89	3.2 ± 1.4	0.2 ± 0.1	6
Karragullen, W.A.	Jarrah open forest	No dominant	6	53 ± 60	3.2 ± 2.8	0.4 ± 0.2	12
Mt Glorious, Qld	Mesophyll vine forest	No dominant	4	100 ± 58	6.8 ± 1.7	0.1 ± 0.1	1
Kununurra, W.A.	Mango plantation	No dominant	5	184 ± 145	2.8 ± 0.8	0.5 ± 0.3	18
Kununurra, W.A.	Mango plantation	*Oecophylla smaragdina*	5	3245 ± 4132	17.4 ± 8.5	15.0 ± 8.5	86
Ghana	Cocoa plantation	*Oecophylla longinoda*	5	4407 ± 5638	50.0	35.3[1]	72[1]
Ghana	Cocoa plantation	*Tetramorium aculeatum*	5	1236 ± 1912	26.2	1.2[1]	5[1]
Ghana	Cocoa plantation	*Crematogaster striatula*	5	3420 ± 5042	17.1	2.1[1]	12[1]

[1] Due to the method of data presentation in the original publication these figures are for the dominant ant only.

genus I have observed holding such territory in northern Australian trees is *Crematogaster* sp. (J. D. Majer, pers. comm.), although its abundance per unit area is far less than that of *O. smaragdina*. Observations indicate that these two species can be dominant in plantations, sclerophyll vegetation and in monsoon forest, thus forming a partial ant mosaic, with large spaces between the territories of dominant ants. Apart from these two ants, my observations throughout the subtropical and tropical monsoonal zones have revealed no additional arboreal species of dominant ant.

DISCUSSION

The sampling methods used are subject to a number of limitations. For instance, the sticky trapping may not sample the true canopy fauna and the chemical knockdown sampling may not reach the upper parts of the canopy, particularly in the tall Queensland mesophyll vine forest. My visual observations and hand collections in the canopy, some of which have been made from an aerial work platform, indicate that both sampling methods provided a reasonable representation of the fauna present in the upper canopy.

The times when observations were made could have corresponded with a period of minimum ant activity. Observations were performed during both the wet and dry seasons at the various study sites so this is unlikely to radically affect the results which are presented here.

The validity of comparing plantations with native rain forests may also be questioned. As mentioned earlier, observations were also made on the native vegetation in the vicinity of the mango plantations. Certainly there were differences in the species of ant present and in the vertical stratification of species. However, the general abundance of ants in the native vegetation was of the same order as that observed in the plantations.

It should be emphasized that I am discussing the tree-nesting ants and the ground-nesters which forage on trees. My findings do not apply to the ground-foraging ant fauna, which is particularly diverse throughout much of Australia (Greenslade 1979, Andersen 1983). In many cases, species of ground-nesting *Iridomyrmex* reach numerically dominant status (Greenslade 1976) with densities comparable to those of dominant species in the tropics.

Two major conclusions may be drawn from these observations. First, the diversity of arboreal ants, both tree- and ground-nesting, is low in Australian rain forests in comparison with other tropical regions and it is sometimes lower than that of the adjoining sclerophyll forest. Second, except where *O. smaragdina,* or perhaps certain *Crematogaster* spp., are present, the trees of the tropical monsoonal and subtropical rain forests in Australia lack dominant tree- or ground-nesting ants. This contrasts with other tropical regions where there is generally a range of dominant species, which occur side by side, thus forming an ant mosaic. A number of possible reasons for the low diversity and low degree of dominance of Australian rain forest ants may be advanced. These are centered around five major themes:

IT IS POSSIBLE THAT SOME OTHER ORGANISM HAS ADOPTED THE ROLE OF DOMINANT ARBOREAL ANTS.—Following an analysis of the guild composition of the chemical knockdown samples described in this study (Majer, pers. comm.), it is apparent that no other group of arthropods is exceptionally abundant in the canopy. Arboreal ants are predominantly predators and/or nectar consumers and no other abundant taxon in my samples fulfilled this role. I therefore conclude that the role of ants has not been taken over by another taxonomic group in Australian rain forests.

THE STRONGLY SEASONAL CLIMATE IN TROPICAL-MONSOONAL AND SUBTROPICAL AUSTRALIA LIMITS THE BUILDUP OF ARBOREAL ANTS.—Unlike the true humid tropics, the Australian wet-dry tropics are characterized by an appreciable variability in the duration, intensity, and onset of the wet season and also a pronounced seasonality of soil moisture (Ridpath 1985). As a result, the biota experiences a change in hydric status from desert-like in the dry season to humid, tropical conditions during the wet season.

It is these dry conditions which may have limited the buildup of Torresian elements of the ant fauna. Indeed, Lokkers (1986) has shown that the distribution of *O. smaragdina* in Australia is limited in its distribution by mean annual rainfall of less than 500 mm, as well as mean minimum temperature. These arid conditions may be more acutely felt by arboreal species which lack the microclimatic buffering effect of soil, a phenomenon which may benefit the nests of ground-dwelling species.

It is then reasonable to ask why members of endemic genera of southern origin have not infiltrated the trees of monsoon or vine forests. The data from the south of Western Australia indicate a paucity of tree-nesting species in temperate Australia, so candidates for an arboreal existence in the tropics would probably need to have originated from ground-nesters. Greenslade (1985) has noted that Australian epigaeic ants are adapted to a wide range of temperatures but in monsoon and vine forests the closed canopy produces a relatively equable and cool temperature regime. It may be this factor which has created an alien environment for colonization by endemic Australian genera. Greenslade (1985) has invoked a similar explanation of the low richness of ground-dwelling ants in monsoon forest within Kakadu National Park, Northern Territory. This suggestion may also explain the relatively high usage of trees in sclerophyll forest of South Queensland (Table 2), as the microclimate would be warmer and less buffered in this more open forest formation.

In summary, it is highly probable that the frequent dry periods have prevented the colonization of rain forest trees by ants of Indo-Malayan origin while the equable and low temperatures have prevented the colonization by endemic genera.

THE PRODUCTIVITY OF AUSTRALIAN TROPICAL RAIN FORESTS AND PLANTATIONS LIMITS THE ABUNDANCE OF ARBOREAL ANTS.—Unfortunately there are little comparative data on the productivity of Australian rain forests or of the abundance of primary and secondary consumer arthropods in relation to rain forests elsewhere in the World. However, inspection of the non-ant component of arthropod biomass in the chemical knockdowns in vine forest at Mt. Glorious (6.7 g) and in mango at Kununurra (2.3–2.4 g) (Table 3) indicates that values are considerably lower than for Ghanaian cocoa plantations (14.7–25.0 g). My own field observations in West African rain forest suggest that arthropods are far more abundant per unit area than in the various Australian rain forests. In addition to appearing to have a lower arthropod biomass than in the true humid tropics, the subtropical Australian vine forest arthropods exhibit a marked seasonal variation in abundance (Lowman 1982). Although this also happens in the humid tropics (Gibbs & Leston 1970), the troughs in arthropod abundance appear to be more marked in Australia (Lowman 1982). On the basis of arthropod abundance and seasonality, I conclude that the arboreal ant fauna could be limited by the relatively low and inconsistent availability of prey items and possibly also homopteran nectar sources.

THE BIOGEOGRAPHIC ORIGIN OF AUSTRALIAN RAIN FORESTS, AND THE ANTS THEREIN, IN SOME WAY LIMITS THE ABUNDANCE AND DIVERSITY OF ARBOREAL ANTS.—

One possible explanation for the paucity of arboreal ants is that Australian rain forests are late invading elements from the "Indo-Malayan" region and, because of the young age of this environment, ants which utilize the canopy of trees have not had sufficient time to evolve. This explanation is not plausible as Webb and Tracey (1981) have demonstrated that Australian rain forests are generally relicts of archaic forests dating back to Gondwanaland times.

Contemporary Australian rain forests are now restricted to a series of pockets extending from Cape York to Tasmania, and less continuously across northern Australia. They were formerly more extensive but have periodically shrunk and expanded as a result of climatic fluctuations. Consequently the relict fragments have become successively isolated and some may have become totally eliminated during previous periods of contraction (Webb & Tracey 1981).

It follows then, that the isolation and frequently small size of these rain forest fragments may have favored the extinction of certain animals, arboreal ants included. Furthermore, the isolation of many of the fragments may render them less accessible to colonization or recolonization by animals such as arboreal ants.

Although there is a possibility that this explanation may be correct, I find it unlikely in view of the absence of a well-developed arboreal ant community in the larger remaining tracts of rain forest in eastern Australia.

ABOREAL ANTS MAY BE LIMITED BY COMPETITION FROM DOMINANT GROUND-DWELLING ANTS.—It is well known that much of the Australian continent is dominated by ground-nesting *Iridomyrmex* spp. (Greenslade 1976, 1985). Preliminary data from sclerophyll forests and woodlands in the Northern Territory suggest that arboreal-nesting species are limited by competition from dominant *Iridomyrmex* spp. which forage on the trees (Greenslade 1985). Could this also be the case in the rain forests? Greenslade's (1985) data and my own observations indicate that *Iridomyrmex* is excluded from or severely limited in rain forests due to the heavy shade cast upon the ground and also by the deep litter. This, together with the fact that few *Iridomyrmex* spp. ventured up the trunks of rain forests in Darwin or southern Queensland (Table 3), suggests that competition with ground-dwelling ants is an unlikely reason for the paucity of arboreal ants in Australian rain forests.

The possible reasons put forward in this paper for the paucity of arboreal ants in Australian rain forests are not conclusive, nor are they mutually exclusive. More than one factor may be responsible for this phenomenon; although it is felt that the strongly seasonal nature of the climate, and also the low and seasonal productivity of Australian rain forests are considered to be the most important factors. There is clearly a need to gather seasonal data on the microclimate and productivity of Australian rain forests in order to compare with such forests elsewhere in the World. Hopefully, this paper will stimulate more research on ants in the Australian tropics and maybe then, when more data are gathered, the reasons for paucity of arboreal ants will become more clear.

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