COMMUNITY STRUCTURE OF ANTS IN BRUNEI RAIN FOREST

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For Moss and Laura Levy,
and in memory of Gertrude Meyer.

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Abstract

This thesis examines the patterns in the ground and low-vegetation ant community of primary lowland dipterocarp forest in Brunei, South East Asia.

The first experimental chapter establishes the importance of ants as the numerically dominant taxon of the forest floor litter arthropod community, how many species were found in a hectare of forest, and the probable minimum asymptotic number of species for each of four sampling methods. The amount of small fragments of litter is found to vary across the plot, increasing in the valley, and best explains differences in species richness of samples. Species richness is highest in the valley. Faunal, rather than microhabitat factors, are found to be the best predictors of certain litter species' abundance.

Chapter three shows that colony dispersion is not a good method with which to investigate competition in this habitat at present. The ground dwelling ant community are more often clumped than over-dispersed, but patterns are impossible to interpret in the light of ecological theory without knowing the biology and population dynamics of the species well. I show by reanalysis that two major flaws in a similar study by Levings and Franks (1982) confound their claim that overdispersion of ant colonies occurs in Panama. This result has implications for many other similar studies of spatial dispersion as evidence of competition.

Chapter four examines whether there is a predictable dominance hierarchy in the bait responsive species foraging in the litter and on tree trunks. No evidence of such a hierarchy was found, although significant temporal patterns unexpected from diel cycles imply avoidance of some species by others. Differences in recruitment ability were found between tree and ground foraging species and these correlated with speed to locate and persistence at baits. A method is offered to test whether ant species are solitary foragers.

Chapter five shows that there is no clear relationship between niche overlaps and association, i.e. avoidance of colonies or foragers at baits. Low temporal overlap and high food overlap were found, but did not appear to be related.

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Contents

with seven plates

CHAPTER ONE

Community structure of ants in Brunei rain forest: an introduction

The Brunei Rain Forest Project 1991-1992

The Brunei Rain Forest Project 1991-1992 was a joint venture between the Universiti Brunei Darussalam and the Royal Geographical Society, London. The Kuala Belalong Field Studies Centre was set up on the west bank of the Sungai Belalong (Belalong river), in the Batu Apoi reserve, Temburong district (details in Cranbrook and Edwards, 1994). The reserve is the largest in Brunei. Over a period of 14 months, more than 60 scientists established baseline data on the biota and hydrogeology of the catchment area. This study is one of six long term post-graduate projects based at the field centre, which continues as a research and education facility today.

Brunei Darussalam

Brunei Darussalam is in north-eastern Borneo, surrounded by the Limbang district of Sarawak, Malaysia. It lies between 4° 02' N and 5° 03' N, and 114° 04' E and 115° 22' E. The land area is 5765 sq. km., with 4692 sq. km., i.e. 81%, still under forest cover, and 59% under primary forest cover. Forest types include: lowland (46.3% of the land area); montane (1.2%); inland swamp (30.4%); and mangrove (3.5%). The reason for this unusually high forest cover is due to Brunei's high oil and natural gas revenue and careful land use and development policies. Annual deforestation is only 50 sq. km. Timber extraction for local use is allowed only under strict controls by the Forestry department, and clear felling is prohibited. There are 11 legally constituted forest reserves, covering 39% of Brunei's land area. Of this area, 86% is primary forest, and 75% of this is dipterocarp rich forest.

The population of Brunei (300,000 people) is mostly urban, except for a few Iban, Dusun, Penan and Murut communities who still hunt and cultivate. The government is now investigating other sources of income in order to diversify the country's economy[1].

Brunei consists of two disjunct parts, the larger western region where the capital city Bandar Seri Begawan is situated, and the smaller eastern region, Temburong, where the fieldwork for this thesis was carried out. Temburong consists of a swampy coastal plain with hilly to montane terrain inland, with the highest peak, Gunung Pagon Priok, at 1850m.

The level of biodiversity in Brunei is very high, because of its nearly equatorial position and abundance of forest types. The high floristic diversity of the area and lack of a strong hunting tradition, except in the few forest dwelling communities, has meant that mammalian and avian diversity is also high. Orang utan *Pongo pygmaeus* have recently been observed for the first time in Brunei (Levy, 1992). Thus, compared to the conservation record of many other South East Asian countries, Brunei is unique in its success in preserving biodiversity. This makes it of particular interest to biologists, particularly as its economic diversity increases and the forests come under more threat.

My field area

The fieldwork for this thesis was performed largely in hectare plot AAU1, an area of primary lowland dipterocarp rain forest on the West Ridge of the S. Belalong. The tree flora has been characterised as 'lowland mixed dipterocarp' (Ashton, 1964). Fig. 1.1 shows the contours of the plot, which consisted of drier ridge top and moister, darker valley areas (Figs 1.2 and 1.3 respectively). Clear patterns were found in the distribution of herbs with respect to location in the plot: two species of *Diplazium* ferns were found to be segregated according to moisture requirements. The dominant tree species was *Elateriospermum tapos*, with 35 individuals. The family Dipterocarpacae, namely *Shorea* spp. accounted for over half the basal area of trees in the plot[2]. There was no disturbed forest within 1km, so that the plot was not subject to edge effects. The work for chapter three of this thesis took place 50m from the north edge of the plot, at two other locations on the West Ridge.

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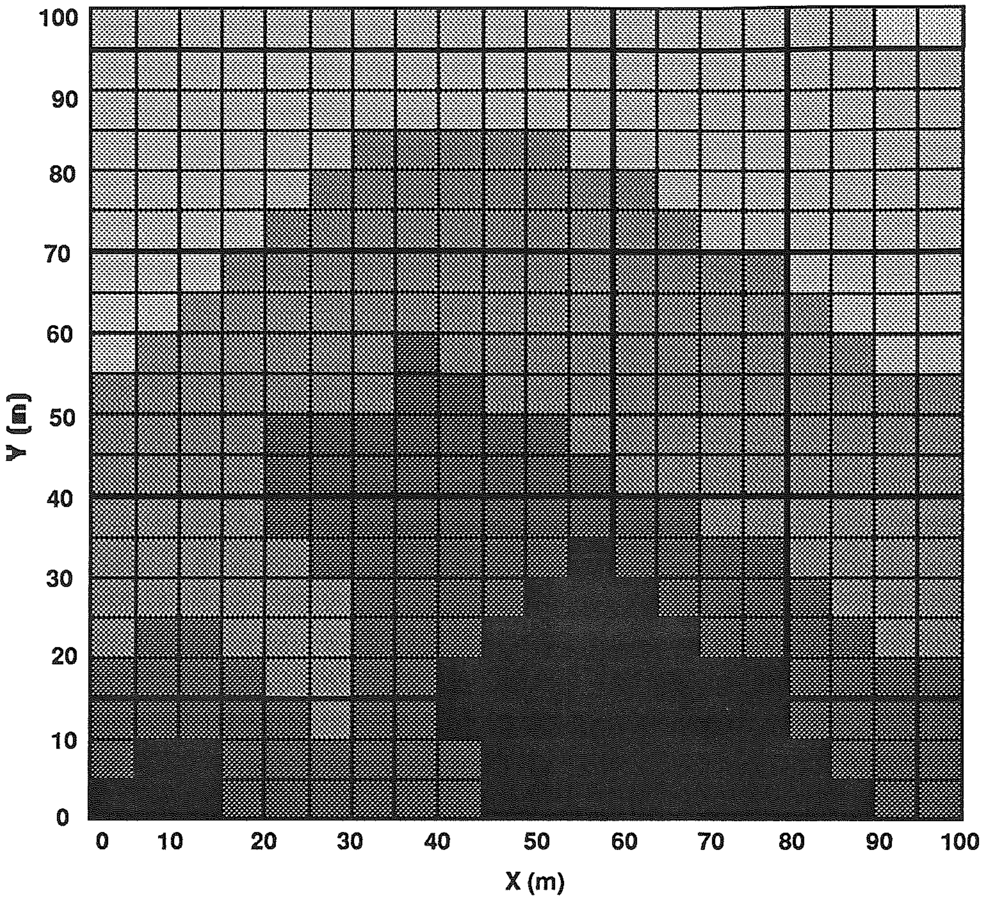
[1] All data from Collins et al. (1991) but see FAO (1988), Sayer and Whitmore (1989), WRI (1990) and Whitmore and Sayer (1992)

[2] All data on plot AAU1 from Cranbrook and Edwards (1994)

Fig. 1.2: Ridgetop area of the plot, with buttress tree in the background

Fig. 1.3: Valley area of the plot, with more luxuriant undergrowth and shade

Fig. 1.1: Contour diagram of plot AAU1: darker shading indicates the valley area, lighter shading the slopes and ridgetop. The x axis faces east. The vertical distance from the highest to the lowest point in the plot is 63.15m.



Tropical rain forests and ants (Hymenoptera: Formicidae)

Tropical moist forests harbour over half the world's species in 7% of its land area (Wilson, 1988a) and are being cleared faster now than at any time in the past (Myers, 1988; Ehrlich, 1988; Sayer and Stuart, 1989; Sayer and Whitmore, 1989; Whitmore and Sayer, 1992; Western, 1992). They are also one of the world's least studied major terrestrial ecosystems (Hammond, 1992). Wilson (1988b) calls for immediate and sustained description of tropical forest biota before it is too late.

The tropical rain forest canopy has been regarded as the unexplored centre of biodiversity (Erwin, 1983), although in terms of the ant fauna, the leaf litter and rotten wood have proved to harbour the richest tropical rain forest fauna (Barry Bolton, pers. comm., and Verhaagh, 1990). Around 1.4 million biological species (allowing for synonymy) have so far been described, of which over half are insects (Parker, 1982), the majority of which live in tropical forests. A global species richness estimate of 30 million species was proposed by Erwin (1982), based largely on extrapolations from work on the tropical rain forest canopy arthropod fauna of Panama. Stork (1988) reassessed the data and proposed a total of up to 80 million. Most other estimates are lower, and vary between three and ten million (e.g. Wilson, 1988a).

Ants are a very large component of the world's animal biota: a recent estimate in Borneo showed that 46% of individuals in tropical rain forest canopy fauna were ants (Floren, in prep.), and estimates have been similar in the Neotropics (e.g. Fittkau and Klinge, 1973; Adis et al., 1984). Wilson (1990) proposes that ants are 50% of the world's animal biomass. So, knowing the structure of tropical ant communities would be an important contribution to understanding the community biology of the world's animal biota.

Community structure: what is it?

As noted by Roughgarden and Diamond (1986) and Giller (1984), it is difficult to give a satisfactory formal definition of a 'community'. Authors often restrict their studies of sections of the entire biotic complement of a habitat to spatially, trophically, taxonomically or life-form delimited groups of species. Giller (1984) adopts Whittaker's (1975) definition, in which a community is a combination of plant, animal, and bacterial populations, interacting with one another within an environment, thus forming a distinctive living system with its own composition, structure, environmental relations, development and function.

What is community structure? Random assemblages of numbers are liable to have predictable patterns, simply from the phenomena of patterns that occur within random assemblages of anything. Roughgarden and Diamond (1986) remind us that patterns in species abundance, body size/ abundance correlations, food web patterns, distributions in eco-morphological space, geographical trends in diversity and many other factors have all been offered as evidence of community structure, but conclude that a good place to begin to look for biologically meaningful structure is in the concept of 'limited membership' (Elton, 1927).

Membership of communities is limited by three main factors: the physical environment, dispersal, and interspecific interactions (Giller, 1984; Roughgarden and Diamond, 1986). The main interspecific interactions are competition and predation (Connell, 1975; Roughgarden and Diamond, 1986). Begon et al. (1986) classify the factors affecting the distribution of organisms into two classes, primary and secondary factors, corresponding broadly to the physical environment and biotic factors. Primary factors include productivity and climatic variability, and some are correlated with latitude and altitude. Other primary factors vary independently of latitude: 'islandness' and frequency of disturbance for example. Secondary factors include predation, competition, spatial heterogeneity created by the organisms themselves, and successional status.

How do these factors affect the numbers of species in a community and their abundances? In most terrestrial biological communities, species diversity decreases with increased latitude (MacArthur, 1972), although there are notable exceptions (such as some wading birds: Giller, 1984). The usual latitudinal pattern is the case for ants (Fischer, 1960). For example there are two ant species in the whole of Finland's tree canopy (Wilson, 1990), yet 43 species in one Peruvian tree (Wilson, 1987), approximately the same number as in the whole of the British Isles.

Other important primary factors include rainfall, temperature and island size. How have these factors been found to affect ant communities? Davidson (1977b) showed that on a longitudinal gradient of increasing rainfall, equivalent to an index of productivity in arid regions, ant species diversity is highly correlated with mean annual precipitation. Torres (1984) cited many studies of ant species distribution and physical factors, concluding that temperature is extremely important in regulating world ant distribution. Torres shows that certain species of forest dwelling ants have different physical requirements from species living in more insolated habitats, which in turn affect their success in combat with other species. Ant species presence is affected primarily by minimum size requirements of islands in the Florida Keys and secondarily by differential competitive exclusion of species (Cole, 1983).

Habitat heterogeneity and stability have been shown to limit species richness in several habitsts, such as Papua New Guinea (Room, 1975). Andersen 1986a, 1986b) found that climate and vegetation structure affect community composition and organisation: mesic and arid faunas differ in composition and in the strength of community structuring forces. Nest sites are an important resource for ants within their habitat: Doncaster (1981), Herbers (1989) and Gallé (1990, 1991) showed that they can limit community species richness, abundance and spatial distribution.

The body of evidence frequently suggests some integration of primary and secondary forces structuring ant communities. Levins et al. (1973) first suggested the integration of immigration and emigration dynamics, local community structure, species autecology, and interspecific behavioural interactions in order to understand coexistence.

Given the role of primary forces in affecting large scale ant community composition in habitats, what of the role of secondary forces in enabling coexistence within given habitats?

Communities and competition

As noted above, competition and predation are the primary biotic factors structuring communities. Connell (1975) selects Birch's (1957) definition of competition:

"Competition occurs when a number of animals (of the same or different species) utilise common resources, the supply of which is short, or if the resources are not in short supply, competition occurs when animals seeking that resource nevertheless harm one another in the process".

Keddy (1989) notes Milne's (1961) definition of competition as:

"...the negative effects which one organism has upon another by consuming or controlling access to a resource that is limited in availability".

Resources are defined by Tilman (1982) as:

"any substance or factor which is consumed by a organism and which can lead to increased growth rates as its availability in the environment is increased".

Most of the world's biotic communities are dominated by large sessile species which compete for space, such as trees, kelps, corals or ant colonies (Connell, 1975). There is usually a mosaic of mature dominants, interspersed with immatures of the same species and other more opportunist species. Roughgarden (1986) and Yodzis (1986) both describe two sorts of species, one of which is sedentary and uses a large proportion of resources from a restricted area, and the other which is more mobile, using a small proportion of the resources from a wide area. The former species are limited by space and tend to form dominance hierarchies (dominance may be defined as: "The possession of high social status within an animal group that exhibits social organisation; it is often achieved and sustained by aggression toward inferior individuals": Allaby, 1992). The latter are limited by food and are more prone towards resource partitioning. Ants and other colonial organisms fall primarily into the former category. Predators and organisms higher in the food chain are also more likely to compete (Keddy, 1989), and much discussion about the non-existence of competition has failed to consider this (Strong, 1984).

Competition usually occurs within trophic levels. It may also take several forms: Schoener (1983) proposed six types, which can be broadly grouped into two kinds: interference and exploitation competition. These two types of competition are both included in the definitions of competition above, i.e. exploitation competition involves direct appropriation of resources by an organism, so that these resources are not available to its competitor. Interference competition occurs when one organism disables another from accessing or utilising the resource.

Connell (1983) and Schoener (1983) review 164 and 72 case studies of community structure papers, respectively, and both find abundant evidence of competition in communities: it occurs in over 50% of cases studied. However, Keddy (1989) notes the problem of bias of subject species chosen for study: to gauge the true importance of competition in communities, one must obviously sample a representative selection of habitats and species. Negative results of competition experiments are often simply not published (Putman, 1994).

Methods of investigating community patterns

Connell (1975) lists three ways of investigating pattern in communities: these comprise description of pattern (such as gradient analysis, fitting mathematical models of relative abundance, and description of niche relations), natural experiments, and controlled field experiments. Roughgarden and Diamond (1986) remind us that there is no community pattern diagnostic of competition, but that presence of patterns predicted by the existence of competition are a useful preliminary indication of the underlying community structure. Whittaker (1967), Levins (1968) and Terborgh (1971) have all used description of pattern to begin to understand underlying community processes.

Ants as model organisms

Andersen (1990, 1991) notes the particular features of ant communities which make them model organisms for the investigation of community structuring processes. They are abundant and readily sampled, their colonies are easily mapped, and their diel and seasonal schedules can be easily observed. Their diet can be ascertained from collecting food items as they enter the nest, and behavioural hierarchies are easily observed at baits. They have features that make them somewhat akin to plants, (such as their usually sedentary colony habit). This is reflected in the experimental methods commonly implemented when studying their ecology (Harper, 1977).

Ant community structure

Wilson (1990) and Hölldobler and Wilson (1990) summarise the phenomena held to be primarily important in ant community structure: intra- and interspecific competition are the main structuring forces. Interspecific interference competition and dominance hierarchies are found almost universally to operate where strong community patterns exist. These phenomena have been investigated by using several approaches: 'natural experiments' and sucessional studies (Brian, 1952; Greenslade, 1971; Franks, 1982; Majer, 1990; Andersen, 1992), manipulative experiments (Cole, 1983; Fox, et al., 1985; Haering and Fox, 1987; Ryti and Case, 1986, 1988), spatial patterning studies (Room, 1971; Majer, 1972, 1976a, 1976b, 1976c, 1993; Leston, 1973, 1978; Briese and Macauley, 1977; Levings and Franks, 1982; Jackson, 1984), niche relationships (Davidson, 1977a, 1977b; Hansen, 1978; Lynch, et al., 1980; Lynch, 1981; Briese, 1982; Torres, 1984; Marsh, 1985; Cerda and Retana, 1990), and interspecific interaction experiments (Brian, 1964; Cole, 1983; Fellers, 1987; Savolainen and Vepsäläinen, 1988). Most of these studies confirm the importance of interspecific interactions in ant community structure, and that hierarchical patterns as described above for sessile communities are the norm. Many authors describe competitive hierarchies in ant communities (e.g. Brian et al., 1976; Lynch et al., 1980; Cole, 1983; Fellers, 1987; Savolainen and Vepsäläinen, 1988). All authors propose two or three level hierarchical ant communities comprising at least:

1) Behaviourally dominant, aggressive and often territorial species
2) other species which are able to exist submissively with the above, and often
3) interactive species which are forced into interspecific encounters with dominants.

Species behaviourally dominant in the community hierarchy have been found to have narrower niches (Lynch et al., 1980), one of three predictions of the hierarchical model of community structure (Keddy, 1989). Another prediction is that species in the hierarchy have inclusive niches, i.e. the gradient is one of resource quantity, with all species having best performance at the same end of the gradient (e.g. more food or light). Lastly, species vary in competitive ability in a predictable manner, and that competitive ability is an inherent quality of species. Increased levels of aggression are often linked to more specific food requirements and/ or richer resources (Hölldobler and Wilson, 1990). These sorts of hierarchies have also been found in bird communities (Pimm and Pimm, 1982; Gretchen Daily, pers. comm.).

The methods listed above are frequently used in combination to understand community processes (e.g. Cole, 1983; Savolainen and Vepsäläinen 1988). More detailed description and discussion of individual studies is given in later chapters.

Gallé (1990, 1991) finds that between habitats, the most important factors governing the structure of north temperate sand dune ant communities are vegetation architecture, surface active invertebrates, availability of twigs and soil and microclimate. Hölldobler and Wilson (1990) and Gallé (1991) say that, where dominants are not found, community structure is less predictable and environmentally mediated.

Dominance impoverishment

Hölldobler and Wilson (1990) and Wilson (1990) state the 'dominance-impoverishment' rule: "the fewer the ant species in a local community, the more likely the community is to be dominated behaviourally by one or a few species with large aggressive colonies that maintain absolute territories".

This has been found to be true in almost all habitats examined, but not so in tropical northern Australia, where dominance occurs with high species richness (Hölldobler and Wilson, 1990).

May (1973) showed that community instability resulted from more complex webs of interaction in communities: The number of interactions in stable model communities is proportional to the actual number of species (M), rather than the number of possible links (M(M-1)). This is the hyperbolic connectance law (Nee, 1990), and means that as species numbers in communities increase, the ratio of actual to possible interspecific interactions decreases. This phenomenon, and weaker interactions, increase stability. This would predict the dominance-impoverishment rule noted above, for stable communities.

Some questions

The relative paucity of detailed studies of ant community structure in the tropics, and especially in South East Asia, leave many questions unanswered. This thesis addresses the following questions:

How many species are there, and what proportion of the arthropod fauna do ants represent in this habitat? I investigate the efficiency and similarity of commonly used sampling methods in accumulating species and numbers of individuals, and offer a model to predict asymptotic numbers of species for each sampling method.

Are species abundance and distribution correlated with microhabitat factors, or with other species occurences? Hölldobler and Wilson (1990) note our lack of understanding of the factors governing the community structure of ant fauna in the litter of tropical forest floors, probably the most diverse ant communities in the world. I use stepwise regression to find the best predictors of the abundance of ten common species occurring in the litter.

How frequently is evidence of competition found in the Bruneian rain forest ant community? Are interspecific interactions weak as predicted? Chapters three, four and five address different aspects of these questions, using spatial dispersion, behavioural interactions and niche relations to answer them.

Is there evidence for competition in the Bruneian rain forest floor ant community? Spatial dispersion patterns of ant colonies have frequently been used by workers to suggest that competition is occurring within or between species. In chapter three I consider the results of a study of this community in the light of two models of competition and their spatial pattern predictions. I reanalyse the data on spatial dispersion of a forest floor ant community in Panama (Levings and Franks, 1982) using a correction factor for edge effects, in order to ascertain whether their claim of significant overdispersion is caused by edge effects or by actual overdispersion.

Is there a behavioural hierarchy in the litter and low vegetation foraging ant community? I look for evidence of hierarchical behavioural interactions of the type found by Greenslade (1971) in Australia, Fellers (1987) in North

American forests or Savolainen and Vepsäläinen (1988) in Finland. What are the behavioural and taxonomic correlates of foraging success at protein and carbohydrate baits? How do patterns differ between tree and litter foraging fauna? These questions are answered in chapter four.

How much do abundant, generalist ant species overlap in their resource utilisation? How true is Sudd and Franks (1987) statement that ants "are, in general, carnivores", and most workers' assumption that species resources overlap greatly? The relationship between niche overlap and competition is examined by looking at the resources food, space and time, and their overlap relative to interspecific nearest neighbour distances, as a measure of interspecific competition.

The function of the Brunei Rain Forest Project 1991-1992 was to establish baseline descriptive data, as a platform for further, more detailed research into the ecology of lowland primary dipterocarp forests. The study is thus primarily descriptive in nature.

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CHAPTER TWO

Ant community diversity and distribution

Introduction

Ants and termites are the dominant faunal component of tropical habitats in terms of numbers and biomass. Fittkau and Klinge (1973) showed that ants comprised about 35% of individuals of the total insect community in the Brazilian Amazonian rain forest. More than 30% of the total insect biomass consists of ants and termites, with ants making up over 85% of all individuals in this fraction. Ants made up 50% of insect individuals in the forest canopy and 30% of all insect biomass (Adis et al., 1984). Ants are 70% of all insects in the forest canopy in Peru (Erwin, 1989), and in Seram, Indonesia, ants were 40% of those in canopy knockdown samples (Stork, 1988), although in subtropical Australia, ants are a smaller component of the arboreal fauna (Basset, 1990). Ants are abundant in Zaïre (Dejean et al., 1986) and in temperate habitats including the Tvärminne Archipelago of Finland: Wilson (1990) proposed that 10% of the insect biomass in the Tvärminne Archipelago is ants, and that world wide, ants are about 50% of the biomass.

In Sabah, Malaysia ants were found to be the most abundant component of the leaf litter invertebrate fauna at 38%, nearly twice that of Collembola (Burghouts et al., 1992). Atkin and Proctor (1988) also found ants a major component of the tropical litter fauna. However, tropical litter is often less abundant in ants: in Seram, Indonesia, only about 7.5 % of individuals in the leaf litter were ants (Stork, 1988), and they are usually less abundant than Acarina, and sometimes Collembola, Coleoptera or dipteran larvae (e.g. Plowman, 1979; Stork, 1988; Strickland, 1945; Frith and Frith, 1990; Nadkarni and Longino, 1990).

My first question was:

How large a component of the Brunei rain forest litter fauna are ants? How does this match other studies?

The diversity of ants, particularly in tropical ecosystems and especially forests is notable (Table 2.1).

Table 2.1: Ant species richness in some tropical forests

author	location	area	genera, species
Wilson, 1959	P.N.G., lowland rain forest	1 square mile	59 genera, 172 spp.
Kempf, 1964	Brazil, rain forest	1 square mile	71 genera, 272 spp.
Bolton, in Room, 1971	Ghana, plantation and forest	1 square mile	63 genera, 219 spp.
Room, 1971	Ghana, plantation	250 square metres	48 genera, 128 spp.
Wilson, 1987	Peru, forest	1 tree	26 genera, 43 spp.
Cover, Tobin et al., 1990	Peru, tropical forest	30000 square metres	64 genera, 256 spp.
Verhaagh, 1990	Peru, forest	10 square kilometres	78 genera, >500 spp.
Chung, 1993	Malaysia, primary and secondary forest	30000 square metres	52 genera, 192 spp.

The number of species in one Peruvian tree compares with 42 species for the whole of the UK (Skinner, 1987). As with most taxa, numbers of species increase enormously towards the equator (Macarthur, 1972). This leads to my second question:

How many species are there in one hectare of Bruneian lowland dipterocarp forest?

This question is necessarily bound up with concerns relating to sampling methodology. I therefore also approach the following two questions:

a) Which sampling methods collect most ants? I offer a model to predict the maximum number of species accumulated by using each of four sampling methods, during the period I sampled.

b) How similar or unique are the species sampled by these methods?

-what would be the best sampling strategy in this habitat to accumulate most species as quickly as possible?

Invertebrate sampling methods depend on the habitat and the particular complement of species the investigator desires to examine. Many studies in tropical habitats to date concentrate on aerial fauna such as moths, beetles and flying Hymenoptera, using techniques such as light or malaise trapping (Frith and Frith, 1985; Wolda, 1987), and canopy fogging (Basset, 1990). Vegetation sweeping (Janzen, 1973) and litter sampling (Levings and Windsor, 1985) are used for fauna at lower vertical strata. Methods specifically for ants frequently involve baits (Greenslade, 1985; Majer and Queiroz, 1990), canopy fogging (Wilson, 1987) hand searching (Cover et al., 1990; Wilson, 1959; Young, 1986) (Andersen, 1986a), quadrat counts (Room, 1975), pitfall trapping (Greenslade, 1985; Andersen, 1986a; Majer and Queiroz, 1990), sticky traps (Majer, 1990), and litter extraction (Cover et al., 1990; Delabie and Fowler, 1990; Majer and Queiroz, 1990).

Levings and Windsor (1982) found that litter extraction by Berlese funnel (Southwood, 1978) extracted ants with high efficacy in tropical forest on Barro Colorado Island, Panama. Olson (1991) tested the efficacy of different sampling methods for collecting litter ants in tropical forest in Costa Rica and found that Winkler extraction (Ward, 1987) was superior to pitfall traps in species richness and abundance of the catch. The sorts of species caught by different sampling methods differed: Winkler extraction of litter gave more small species and more specialists than pitfall traps.

It is widely accepted that pitfall traps can be useful in enumerating species numbers, but are unreliable in indicating true relative abundances (Andersen, 1986b), due to species' behavioural differences and other factors causing differential susceptibility to capture (Andersen, 1991; Southwood, 1978). In Australian tropical savannah, pitfall traps and quadrat counts were found to give comparable results for the presence of commoner species, although their abundances differed (Andersen, 1991). Romero and Jaffe (1989) found that in Venezuelan savannah, a combination of pitfall trapping and hand searching was the most time efficient way to ascertain the number of species, out of all the methods they used.

Due to the colonial nature of ants, it has been found that abundance of species is best estimated by numbers of samples in which they are present rather than numbers of individuals (Andersen, 1991; Romero and Jaffe, 1989). Room (1975) proposes that frequency of capture makes cross-ecosystem comparisons of ant fauna possible. This approach was taken a stage further by Klimetzek and Pelz (1992), who recommended nest counts above trapping as a ten times more efficient method of ascertaining species diversity. This method effectively recognises the colony as the individual unit, an approach complying with Wilson's view of the colony as the functional unit in ant communities (Wilson 1990).

Although ant colony distributions can be affected by intra- and interspecific interactions, microhabitat can also have an important effect: Bernstein and Gobbel (1979) show that dispersion of ant colonies in North American deserts is notably affected by vegetation structure which alters shading and hence suitable nest sites between elevations, and shows evidence of interspecific over dispersion only at elevations with less vegetation. Gallé (1990, 1991) showed that vegetation architecture, loose wood (nest sites) and ground/ surface foraging fauna influence community structure. Doncaster (1981) found that lack of nest sites on Ramsey Island, Wales, resulted in a contagious distribution of nests, and Brian et al. (1965) showed that in a Southern English heath, ant colonies were distributed according to sunlight levels, drainage requirements and vegetation cover. There are few studies looking at the spatial distribution of tropical rain forest litter species (Hölldobler and Wilson, 1990), apart from a study of forest litter microhabitat preferences in Papua New Guinea (Wilson, 1959), who found a predictable succession of genera in dead wood of different conditions, and a study of the vertical stratification of species in Brazilian cocoa plantation leaf litter: superficial layers were richer in species (Delabie and Fowler, 1990).

My final questions were:

Which ants are in the community and how are they distributed?

a) How are the fauna vertically stratified?

b) Is there evidence for patchiness in the diversity or distribution of species?

c) Which 'functional groups' are where: which methods best sample specialist, cryptic and generalist species?

Methods

FIELDWORK

Fieldwork was conducted over the periods June - December 1992 and April - July 1993. Four sampling methods were implemented, based on the methods used by other workers in the field, especially in tropical forests (see introduction): Winkler litter extraction, pitfall trapping, hand searching of vegetation and baiting over several hours.

Winkler litter extraction

This took place in August 1992. The method was chosen in preference to Berlese extraction, commonly used by other workers, as it was found to be highly effective in preliminary trials, takes up less space and requires no electricity supply. I collected $0.25m^2$ sampling units of leaf litter from each of 100 stratified random points in the hectare, by choosing 10 random squares in each row of the hectare and further coordinates in each square, using random numbers generated on a scientific calculator. The litter was rapidly scooped from the demarcated quadrat and into a large plastic bag which was closed securely after labelling. Large arthropods were caught before escaping. At each point, a separate and smaller sample was collected for litter moisture measurement. This is necessary as processed litter loses volume. The litter and moisture sample were then weighed and the litter sieved in the laboratory using a sieve made of a wooden frame of depth 20cm with a wire mesh at the bottom with holes of 1cm diameter. The sift was weighed and placed inside 1-4 mesh bags depending on its volume. These were hung inside a framed canvas sac for 24 hours with a bottle of 80% ethanol at the bottom, into which insects fell or crawled from the mesh bags. The moisture sample was sun-dried and re-weighed, and its moisture content used to calculate the moisture content, and hence dry weight, of the litter. Arthropods were sorted to order and ants to morphospecies. Immatures of all orders were included in the overall counts for their order. The Winkler method is described by Ward (1987).

Pitfall trapping

This took place in June - July 1993. Large plastic screw top jars of depth 15cm and diameter 15cm were sunk at 100 random points in the plot. The same method of location was used for pitfall traps as for litter samples. Different coordinates were used for the two methods. The traps were filled to a depth of 2cm with a weak soap/ sodium chloride solution, which both stopped insects escaping once in the trap and stopped them bursting by osmosis before collection. No other preservative was used. Each trap was covered with a plastic roof which was tied to neighbouring vegetation, to keep out fallen leaves, which would allow ants to escape. The traps were collected 24 hours later, and all specimens sorted in the lab. Each site was sampled once only. Baited pitfall traps were originally tried but most were destroyed by wild animals.

Vegetation sampling

I sampled vegetation ant fauna in June - August 1992. Ten transects were walked through the plot, one in each 10m wide row. Each transect was sampled on three separate occasions. Ants were collected by hand up to 1.5m away from the transect line in either direction and up to a height of 6.5 feet. All low vegetation and tree trunks were sampled. Each 10m stretch sampling unit was put in a separate vial. Where ants occurred in high abundance, absolute abundance was noted and fewer specimens collected.

Bait sampling

See chapter 4 for a description of the sampling method. Each point over the course of a day was counted as a separate sampling unit. Species were noted only as present or absent. For analysis of vertical segregation of species, tree and ground baits were separated.

ANALYSES

Investigation 1: How numerically dominant are ants?

Specimens in 50 pitfall traps and 50 litter quadrats were sorted to order or major group. Percentage contributions of each order or group to the faunal complement were calculated. Spearman rank correlation was used to see if relative abundances of arthropod groups are more similar than expected randomly in pitfall traps and litter samples.

Investigation 2: How many species are there?

a)Which sampling method collects most ants ? A model.

In order to estimate the asymptotic number of species for each of the four sampling methods, data on numbers of new species collected with each new sample (species/ effort) were assembled. As the raw data were step-like due to spatial or temporal non independence of consecutive sampling units, I randomly resorted and recalculated 100 times to smooth out the species/ effort curve. An exponential model was fitted to the means of these values:

$$y = a\left(1 - e^{-k_1 x}\right) \quad \text{(eq. 2.1)}$$

The fit of this model was found to be poor in terms of k: in all cases, sums of squared differences of the empirical data and the model were over 100, and usually around 500. A second model was tried:

$$y = a\left(1 - e^{-k_1 x}\right) + b\left(1 - e^{-k_2 x}\right) \quad \text{(eq. 2.2)}$$

The model describes two curves which are overlaid, each representing a different set of the fauna, where, for equations 2.1 and 2.2:
y = cumulative number of species for
x = cumulative number of sampling units, and
a and b = asymptotes (maximum number of species) of two curves (sets of species) and
k_1 and k_2 = rates of curvature (speed of accumulation of the two sets of species).

The model was constrained as follows: in all 4 cases, $b>a>0$; $k_2>k_1>0$; $b+a$ (total possible number of species for the sampling method) > total number of species found by myself by field sampling.

The two curves represent two sets of species which are differentially susceptible to appearing in sampling units: the first set are greater in number but harder to find, occurring in few sampling units, accumulating slowly. The second set are fewer in number, but easier to find, occurring many sampling units, accumulating quickly.

The model was fitted to the randomised data by altering a, b, k_1 and k_2 within the constraints until the sums of the squares of the differences between the fitted and empirical data was minimised. The sums of squared differences was always below 30, so that I was able to use it to predict the total expected number of species for each sampling method, and the number of samples required to accumulate them. These figures would represent the minimum possible number of species, as other even rarer species may be present in the community, which would cause the species effort curve to continue rising with further sampling, and others which would migrate in to the area with time.

b) How similar/ unique are the fauna sampled by these methods?

i) Three similarity indices were used to ascertain the relative similarity of the fauna caught in pairs of sampling methods: the Jaccard coefficient, which is a ratio of species common to both sampling methods to all species, the Baroni Urbani and Buser coefficient, and the simple matching coefficient, both of which are ratios using negative as well as positive matches (Krebs, 1989; Spellerberg, 1991). All three methods are binary and thus do not take into account abundances of species.

ii) The percentages of species unique to each sampling method were calculated to assess the best sampling strategy for collection of as many species as efficiently as possible using these methods.

Investigation 3: How are the ant fauna distributed? How do fauna differ between sampling methods?

a) How are species vertically stratified?

I used a G-test (Sokal and Rohlf, 1969) to test whether there were significant differences among subfamilies in the proportions of species and genera found on vegetation only, on the ground only, and on both.

b) What is the spatial distribution of species on the ground and in the litter?

As the part of the plot in the valley was visibly different floristically, and in terms of moisture, to the ridgetop (Cranbrook and Edwards, 1994), I looked to see whether these differences affect the diversity and abundance of the ant fauna in samples of leaf litter and pitfall trap fauna. I used two tailed t-tests to compare the species richness and numbers of individuals in the lower valley area of the plot, with their values in the rest of the plot comprising better drained slopes and the ridgetop. As significant results were found only for the litter samples, I proceeded to examine the roles of litter weight and structure on the richness and abundance of the fauna using multiple regression. Continuous variables were log transformed. I then used two tailed t-tests to see how the important factor varied with location in the plot.

Factors affecting individual species distributions were examined using forward stepwise regression. Twenty-one litter sample, environmental and faunal factors were used to predict the abundance of the 10 commonest species, all occurring in at least 15% of sampling units (table 2.1).

Table 2.1: Factors used in stepwise regression to predict the abundance of the 10 commonest species

litter sample factors:
litter weight
litter dry weight
sift weight
% moisture
environmental factors:
ridge or valley
presence of a tree over 12 feet within 2m
presence of a log over 10cm diameter within 1.5m
presence of stones beneath the quadrat
presence of a root within 1m
presence of a buttress root within 1.5 m
overall measure of microhabitat heterogeneity*
faunal factors:
presence/ absence of *Lophomyrmex bedoti* sp.181
presence/ absence of *Tetramorium* sp. 89
presence/ absence of *Pseudolasius* sp. 46
presence/ absence of *Pachycondyla* sp. 146
presence/ absence of *Odontoponera transversa* sp. 3
presence/ absence of *Strumigenys* sp. 65
presence/ absence of *Tetramorium* sp. 93
presence/ absence of *Camponotus gigas* sp. 1
presence/ absence of *Pheidole* sp. 204
presence/ absence of *Strumigenys* sp. 72

*this consisted the sum of scores for all separate environmental variables except "ridge or valley".

c) Which sampling method best samples cryptic species, trophic specialists, generalists, etc.?

The qualitative nature of the fauna trapped in all sampling methods, namely the distribution of their trophic habits and lifestyle, if known, were examined. Species in the genera *Srumigenys, Harpegnathos, Odontomachus, Anochetus, Myopias* and *Myrmoteras* can all be identified as specialist feeders due to their long, recurved mandibles (Hölldobler and Wilson, 1990). *Acropyga, Cerapachys, Leptogenys* and *Pachycondyla* also have specialist foraging habits. Many species are very small, may have small eyes and rarely emerge out onto the open ground: these are usually regarded as cryptic species. These include the genera *Smithistruma, Hypoponera, Cryptopone, Ponera, Eurhopalothrix, Oligomyrmex* and *Plagiolepis*. Specialists are often also cryptic. Bait responsive species are usually regarded as generalists.

Results

Investigation 1: Numerical dominance of ants

Ants were found to be the most abundant taxon in both the pitfall and litter samples (table 2.2 and figs 2.1 and 2.2) at ~45% of individuals in both cases.

Table 2.2: Numbers and percentages of individuals in major groups found in Winkler litter extraction and pitfall traps.

taxon	pitfall		litter	
	number of individuals	% of individuals	number of individuals	% of individuals
Acari	98	3.07	871	22.80
Anoplura	0	0.00	1	0.0
Araneae	46	1.44	48	1.26
Blattoidea	3	0.09	7	0.18
Coleoptera	240	7.52	558	14.61
Collembola	951	29.81	65	1.70
Dermaptera	0	0.00	2	0.05
Diptera	247	7.74	29	0.76
Hemiptera	30	0.94	34	0.89
Hymenoptera: Formicidae	**1420**	**44.51**	**1732**	**45.34**
Hymenoptera: others	48	1.50	11	0.29
Isopoda	13	0.41	50	1.31
Isoptera	16	0.50	26	0.68
Lepidoptera	2	0.06	28	0.73
Myriapoda	7	0.22	209	5.47
Neuroptera	0	0.00	2	0.05
Opiliones	7	0.22	7	0.18
Orthoptera	45	1.41	6	0.16
Phasmida	0	0.00	1	0.03
Protura	0	0.00	2	0.05
Pseudoscorpiones	8	0.25	58	1.52
Psocoptera	1	0.03	0	0.00
Thysanoptera	2	0.06	29	0.76
Thysanura	0	0.00	2	0.05
Trichoptera	0	0.00	2	0.05
unknown	6	0.19	30	0.79
TOTAL	3190		3810	

Spearman rank correlation showed a strong positive relationship between values in pitfall and litter traps: $p<0.0001$. Pitfall traps are therefore good indicators of actual relative abundances of major arthropod groups found in litter samples, in this habitat. However, inspection of figs 2.1 and 2.2 below shows that abundances of major groups other than ants, especially Collembola and Acari, differ greatly between sampling methods.

Fig 2.1: Pie chart showing contributions of major arthropod groups to the pitfall trap sampled fauna. Minor groups are all plain grey

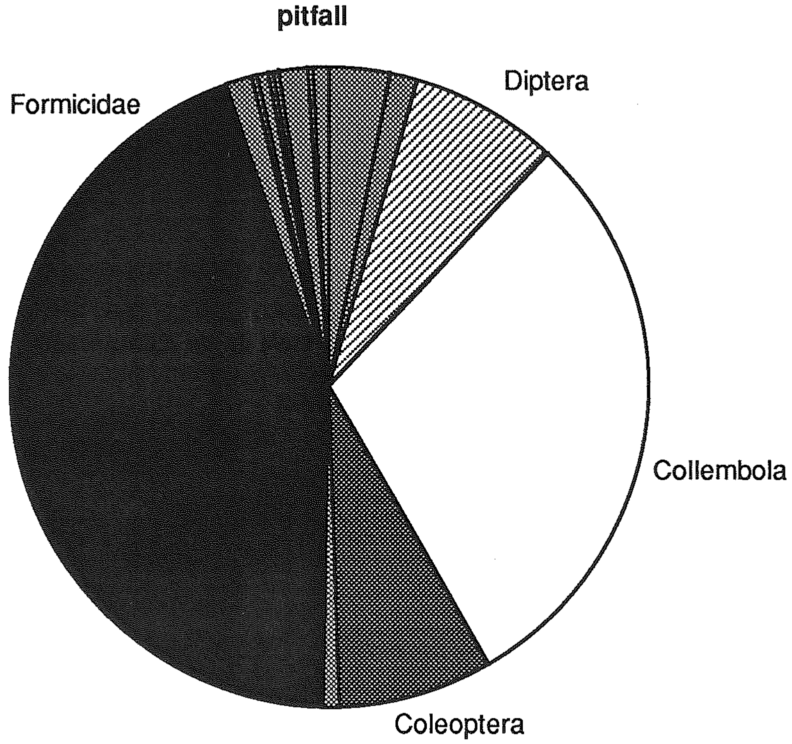
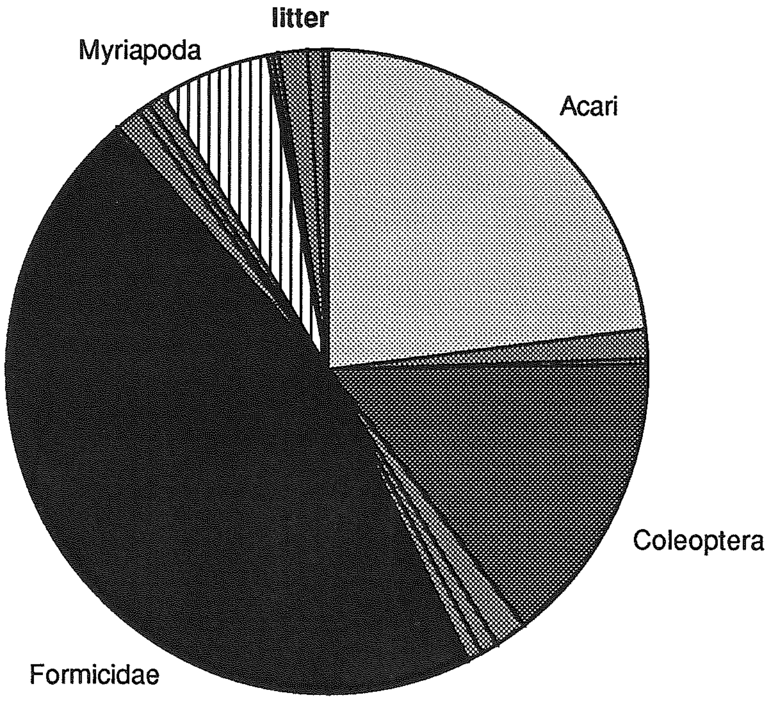


Fig 2.2: Pie chart showing contributions of major arthropod groups to the litter sampled fauna. Minor groups are all plain grey



Investigation 2: How many species are there?

A table of all species and sampling methods is given in appendix 2. A total of 225 morphospecies was collected in the 4 sampling methods discussed in this chapter. Seven other species were found during the fieldwork for the following chapter: these are highlighted in chapter 3. The total number of genera is 57, and of species is 232. Morphospecies separations were checked by Mr. Barry Bolton at The Natural History Museum, London, and a representative collection has been deposited there, and at The Brunei Museum, Jalan Kota Batu, Bandar Seri Begawan, Brunei.

Fig. 2.3 shows the raw species/ effort curves for the four sampling methods. The step-like appearance of the curves was due to some non-independence between samples which were spatially or temporally close to each other. Fig 2.4 shows the mean of the raw data randomised and resampled 100 times, in order to smooth the this pattern.

Fig 2.3: Raw species/ effort curves for the four sampling methods

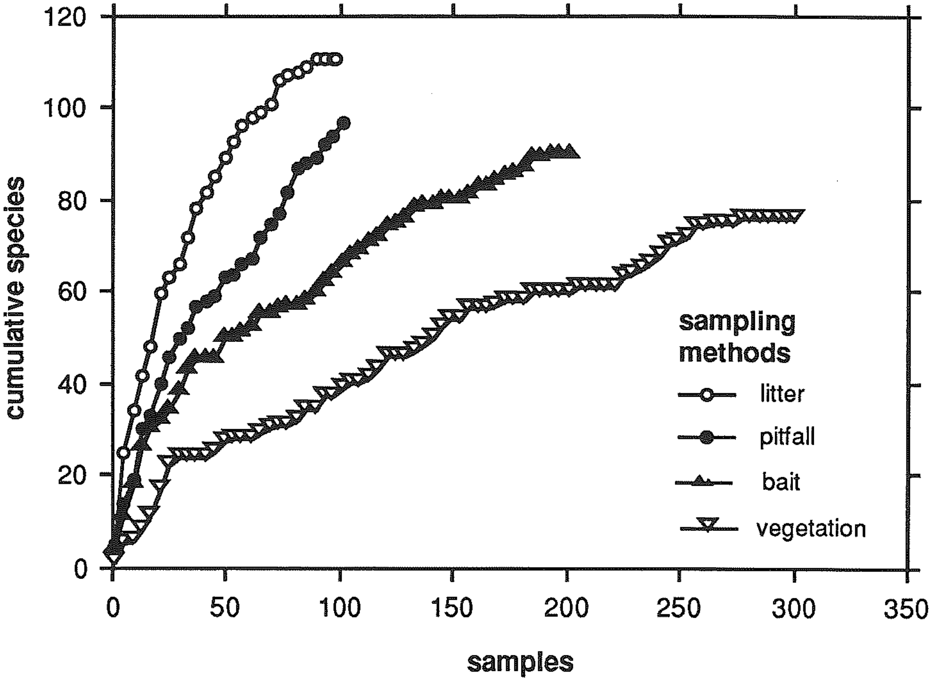


Fig. 2.5 shows the species/ effort curves for the fitted model.

Fig 2.4: Results of randomising and re-sampling the raw data 100 times

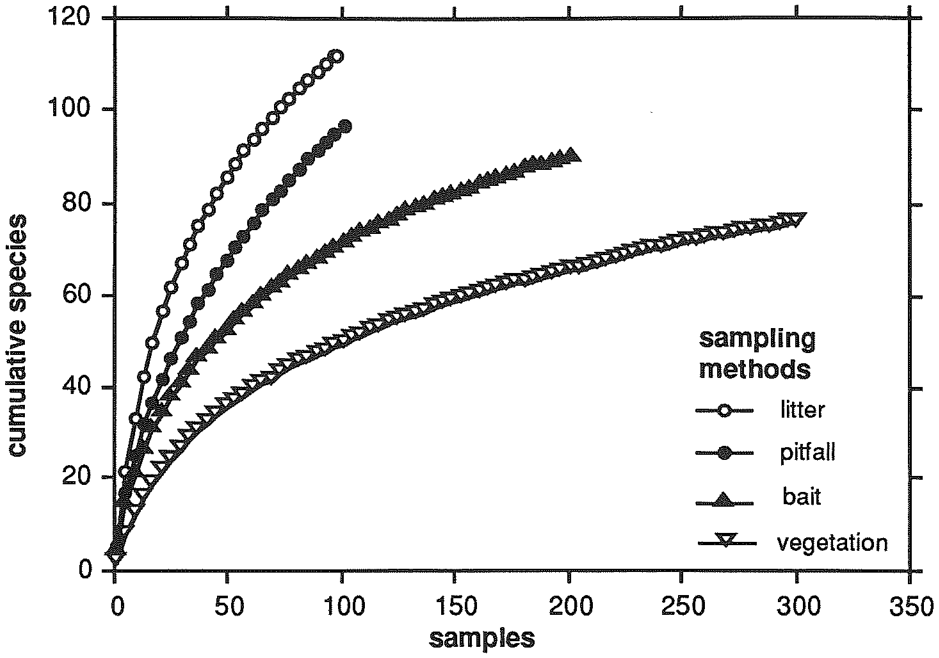


Fig 2.5: Species effort curves of the fitted model

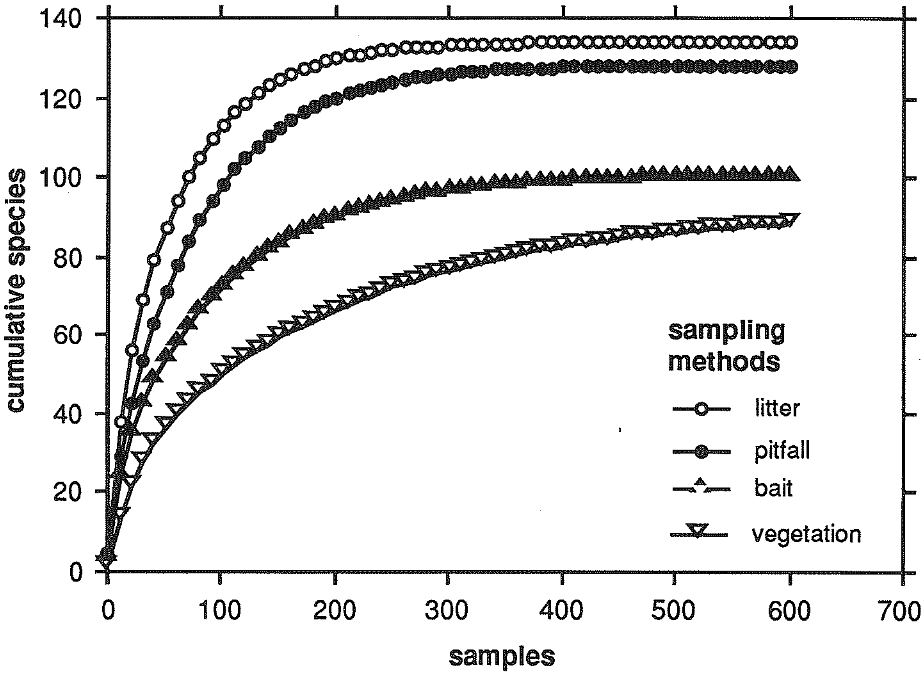


Table 2.3 shows the number of species found, and results of fitting the model to the randomised and resampled data.

Table 2.3: Number of species found, asymptotic number of species, and number of samples to find 95% of these, predicted by the model for four sampling methods, and sum of squared differences between my data and the model, a measure of the closeness of fit of the model.

	vegetation	litter	pitfall	bait
number of species found	76	120	97	90
asymptotic number of species	91	133	128	100
samples to find 95% of species	541	173	220	274
sum of squared differences between my data and the model	19.53 for 300 empirical data points	5.66 for 100 empirical data points	8.51 for 100 empirical data points	27.96 for 200 empirical data points

b) The three similarity coefficients showed that ground bait and tree bait, and bait and vegetation are most similar, and litter and vegetation fauna are most different (table 2.4).

Table 2.4: Similarities of fauna across all sampling methods, giving three coefficients and the mean of these, in descending order of overall mean similarity of the three coefficients.

	Jaccard	simple matching coefficient	Baroni and Buser	mean similarity
ground bait/ tree bait	0.42	0.77	0.68	0.62
tree bait/ vegetation	0.29	0.71	0.57	0.52
ground bait/ vegetation	0.30	0.64	0.54	0.49
ground bait/ pitfall	0.31	0.60	0.53	0.48
litter/ pitfall	0.29	0.50	0.47	0.42
ground bait/ litter	0.24	0.48	0.43	0.38
tree bait/ pitfall	0.15	0.54	0.37	0.35
tree bait/ litter	0.10	0.42	0.28	0.27
pitfall/ vegetation	0.09	0.40	0.26	0.25
litter/ vegetation	0.06	0.27	0.17	0.17

Litter, pitfall and vegetation sampling methods all sampled a high proportion of species unique to them (table 2.5). Baits did not, but their similarity to fauna in other sampling methods should make them a good tool to investigate the interactions of species found in the community by other methods (see chapter four).

Table 2.5: Percentages of species unique in five sampling methods

sampling method	tree bait	ground bait	litter	pitfall	vegetation
% of unique species	6.25	7.79	49.11	32.61	44.44

The most efficient sampling regime to accumulate as many species as possible would be to use the methods of litter extraction, pitfall trapping and vegetation sampling. This should be done for at least the number of samples in table 2.3 to acquire 95% of all species.

Investigation 3: Faunal distribution

a) The G-test on subfamily distribution at two vertical levels showed that vertical distribution is dependent on subfamily membership ($G = 54.9$, d.f. = 2, $p < 0.005$) over all sampling methods. Formicinae were found to occur more on vegetation than the ground or both levels, and Ponerinae were found to occur more on the ground than vegetation or both levels. Myrmicinae were distributed as random over both levels. A more detailed account of species distributions can be found in appendix 2.

b) Litter fauna was more abundant in the valley of the hectare (table 2.6), and species richness tended towards the same pattern, although the effect on species richness was on the borderline of significance. As a preliminary test, this result is worth further investigation.

Table 2.6: Results of t-tests showing that litter ant fauna species richness tends to be higher in the valley areas of the plot. Abundance differs significantly.

Y	factor	p	direction of pattern
log pitfall species richness	valley/ ridge	0.21	valley richer
log pitfall abundance	valley/ ridge	0.57	valley richer
litter species richness	valley/ ridge	0.05	valley richer
log litter abundance	valley/ ridge	0.02	valley richer

Multiple regression was used to examine the contributions of litter weight, litter dry weight, % moisture, and sift weight (from the sift created during the Winkler extraction process) to variation in species richness and abundance of litter samples. Sift weight was the only factor to explain significant amounts of variation in species richness, and abundance (table 2.7).

Table 2.7: Relationship of species richness and abundance with four factors pertaining to the litter samples.

	species richness		abundance	
factor	pattern	p	pattern	p
log litter weight	none	0.63	none	0.66
log litter dry weight	none	0.73	none	0.94
log sift weight	positive	0.005	positive	0.001
log % moisture	none	0.53	none	0.75

As sift weight explained most variation in species richness and abundance, and litter species richness and abundance were higher in the valley, how did sift weight and the other factors vary from ridge top to valley? t-tests were performed on the four variables' variation between ridge top and valley: sift weight almost significantly changes across the plot, whereas none of the other factors are significant (table 2.8).

Table 2.8: Results of t-tests on the variation of four variables with location in the plot

Y	factor	p	direction of pattern
log sift weight	valley/ ridge	0.05	higher in the valley
log % moisture	valley/ ridge	0.78	higher in the valley
log litter dry weight	valley/ ridge	0.34	higher on the ridge
log litter weight	valley/ ridge	0.15	higher in the valley

Sift weight is a measure of the litter structure: it increases with the amount of small sized particles i.e. decomposing matter in the sample. This is more important in its effect on the species richness and abundance of leaf litter fauna than any other factor.

Table 2.9 shows the results of forward stepwise regression of sample, microhabitat and faunal variables as predictors of the abundance of 10 of the commonest species (as measured by numbers of sampling units of occurrence).

Table 2.9: Predictive factors of abundance from stepwise regression for 10 common species

species/ genus	sp. no.	factors	F value	direction of interaction
Lophomyrmex bedoti	181	sp. 146	5.37	-
Tetramorium	89	litter weight	13.80	+
		litter dry weight	8.26	-
		sp. 65	5.74	+
		sp. 204	4.47	+
Pseudolasius	46	litter dry weight	8.63	+
		sp. 181	5.38	-
		sp. 65	5.11	-
Pachycondyla	146	sp. 72	4.67	+
Odontoponera transversa	3	sp. 1	7.20	+
		sp. 93	6.13	+
Strumigenys	65	sp. 89	7.16	+
Tetramorium	93	sp. 89	7.40	+
		tree buttress	5.25	+
Camponotus gigas	1	sp. 204	5.35	+
Pheidole	204	sp. 89	4.25	+
Strumigenys	72	sp. 65	6.26	+

The results show that the presence of other species is more often the best predictor of the abundance of a given species than are sampling unit or other environmental variables: It is possible to test the prevalence of faunal rather than environmental factors in the predicting variables, in the following way: there are 10 analyses (one for each species), 7 environmental variables, 4 litter sample variables, and 9 species variables = 20 variables. If they appeared randomly in the list of primary predictors then species variables should be primary predictors 9 x 10/ 20 = 4.5 times, and litter/ environmental variables 11 x 10/ 20 = 5.5 times. A χ^2_1 goodness of fit to these values gives a value of 4.94 and $p<0.05$. Species variables are therefore more often primary predictors of the abundance of other species than environmental variables.

Furthermore, we can test the numbers of positive and negative interspecific interactions with a sign test, i.e. with 11 positive, and 2 negative, $p<0.05$. Species are thus more often positively associated than negatively associated with other species. It is possible that positive associations of species are due to other confounding variables, but these are not variables that I measured.

c) Inspection of appendix 2 shows that out of 58 species of the specialist and cryptic genera mentioned, 41 species appear in litter samples, 23 in pitfall trap traps and 4 on ground baits. One individual of *Strumigenys* occurred on vegetation, and no cryptic species or specialists on tree baits. *Strumigenys* is extremely abundant in the litter. The species caught in pitfall traps are mostly larger Ponerinae of the genera *Pachycondyla* and the large 'army-ant' type *Leptogenys*. There is thus strong evidence that the litter layer is the richest in species of specialist foraging habit and cryptic lifestyle.

Discussion

The numerical dominance of ants in the litter in the current study is in agreement with Burghouts (1992) and Atkin (1988). However, most other studies have found that Acari, Collembola, or Coleoptera are the major components of the litter fauna. Frith (1990) in Australian upland tropical rain forest, and Plowman (1979) also in Australia, both used Berlese funnels, and neither found ants to be the major faunal component of the litter. Nadkarni (1990) used Winkler extraction in Costa Rica and found ants to be the third most dominant taxon. Stork (1988) does not specify his methods in Seram, Indonesia, but found ants to be a relatively minor component of the litter fauna. Burghouts (1992) sorted litter samples from Sabah, Malaysia by hand, and found ants the most numerous taxon. It is not clear whether these results are dependent on geographical region or sampling method. Initial results thus suggest that northern Borneo has a particularly abundant litter ant fauna relative to other taxa, but comparison with studies in other geographical areas is difficult due to methodological inconsistencies. A comparison of Berlese and Winkler litter extraction in this habitat is needed for more informative comparisons.

Two hundred and thirty two species and 57 genera fits in terms of species diversity with other studies in tropical forests. This number is higher than the 192 found by Chung (1993) in Sabah, Malaysia. This could be because of methodology, as he used baited pitfall traps, soil extraction and vegetation sampling, and so missed many of the numerous cryptic litter species, but may also be due to the proximity to and inclusion of degraded forest areas in his sampling area. The results may imply that the proximity of primary to secondary forest affects diversity in the primary forest by edge effects. He sampled for a longer period than myself, one year, so this result is particularly surprising.

My figures do not, however include the tree canopy fauna which may be somewhat different in nature, with fewer Ponerinae, and many more Formicinae and Myrmicinae. I have underestimated these species. In a preliminary canopy fogging experiment by Nigel Stork in Brunei in 1982 (pers. comm.), 99 species of 29 genera were found on 11 trees. Three genera found in the current study, representing five species, were not found by me at ground or low vegetation level: *Solenopsis, Leptothorax* (both Myrmicinae) and

Platythyrea (Ponerinae). The sample was characterised by extremely high numbers of *Polyrhachis* species: 30 in all.

It may be possible to use the estimated asymptotic numbers of species found by each sampling method in a way that combines these estimates and can be used to predict a single asymptotic number of species for all sampling methods combined, bearing in mind changes in overlap of species and numbers of unique species in sampling methods with different sample sizes.

High similarity of tree and ground bait fauna may be expected due to the possible non-independence of species attracted from one level to another at baits. The low similarity of bait and litter samples is due to the higher numbers of specialist species in the litter: these, almost by definition, are not or are rarely bait responsive. They also run around on the open ground less, so that similarity of pitfall and litter fauna is not very high, despite being closely spatially approximated. All these indices are subject to sample size effects, but are all highly correlated with each other when tested with Spearman rank correlation: in all cases $p<0.008$. Krebs (1989) offers a way of correcting values for sample size differences.

The low numbers of species unique to the bait sampling method affirms its use as a valid tool in the investigation of interspecific behavioural interactions of generalist species in the rest of the community. High numbers in the other sampling methods indicate them as good ways to accumulate species in faunistic studies, such as those employed in ecological monitoring situations. In combination with the model offered to estimate asymptotic species numbers, this study shows that it is possible to ascertain minimum numbers of ant species relatively quickly using these methods. The present results may of course have differed had they been taken at a different time of year. My litter and pitfall samples were taken in a different year, but the same season. This may have caused decreased similarity of the samples, but I feel that this is unlikely: there is evidence to suggest that in Borneo, seasonal variation in ant species composition and abundance is small (Chung, 1993).

Pitfall traps are the best way to catch a section of the fauna difficult to catch by any other method such as large, nocturnal Ponerinae that range over large distances, *Leptogenys*, for example. I found in this study that some arboreal species, namely some recruiting *Polyrhachis* and *Camponotus* also fall into pitfall traps, reducing the worry that their occurrence on ground baits was simply due to their attraction from trees to baits close by on the ground. Pitfall traps thus form a useful addition to other sampling methods, due to their integrating samples caught over time, which none of my other methods did.

Stork's finding of relatively high numbers of Formicinae and Pseudomyrmecinae (*Tetraponera*) in the canopy is similar to patterns elsewhere in the tropics (Barry Bolton pers. comm.). My study reflects the pattern of high formicine numbers on vegetation.

The higher species richness and diversity in the lower and damper valley area and in litter sampling units with more decomposed matter (sift) corresponded with a higher mean sift weight in the valley. This fraction of the litter appears to be important as a source of living space for many species, and to allow many species to coexist. This has important implications for maintenance of biodiversity of litter fauna in degraded or managed forests in South East Asia, where litter cover may be reduced. However, Belshaw and Bolton (1993) found that ant species diversity and abundance in Ghana was not reduced fron primary to secondary forest and cocoa plantation. Delabie's (1990) results in cocoa plantation were in contrast to my own: he found that superficial litter was richer in species. Wilson (1959) found that the richest concentrations of ant species were in the last 2-3 stages of decomposition of small pieces of wood, and that all stages were characterised by certain species of ant living there.

The value of the stepwise regression in assessing the factors predicting the abundance of species is questionable. All F-values are relatively low, and with the large number of variables used, one or two significant variables would be expected by chance from each analysis. There is no outstandingly clear pattern here. It is likely that ant abundances are positively correlated with other ant abundances for reasons of nest site or other resource availability. There is no evidence of any negative interactions at this level, although factoring out the overall positive relationship of ant species with each other may reveal such patterns at a lower level.

Bolton has classified the fauna in Stork's study by feeding habit: all the large Dolichoderinae (*Dolichoderus*), Formicinae (*Polyrhachis* and *Camponotus*) and the abundant *Crematogaster* species are classed as opportunist feeders. Specialists include all Ponerinae and most small Myrmicinae, except *Pheidole*, *Monomorium* and *Crematogaster*. Stork is likely to have underestimated the species living in tree shelf litter, inside vines etc. Many of these may well be specialists, vine species tending scale insects for example. I will have underestimated the species living deep inside large and hard pieces of dead wood. Earlier hand dissection of 10 m^2 of litter revealed many small species of *Pheidole*, and *Strumigenys* living inside pieces of wood as narrow as 3mm wide. Such nests included one or more queens, brood and workers. The potential for diversity in the litter is thus enormous. The litter provides much space for nesting sites and the evolution of specialist life habits, as was shown in this study and that of Olson (1991).

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CHAPTER THREE

Colony dispersion patterns in two rain forest ant communities

Introduction

Hutchinson (1953) was one of the first scientists to consider the importance and causation of spatial pattern in communities: extrinsic factors such as temperature or wave action, and intrinsic social, interactive or reproductive factors may all influence the spatial patterning of populations of organisms.

Plant ecologists have long been concerned with the spatial dispersion of plants as an indication of community structure processes (Kershaw, 1973; Greig-Smith, 1983), and Andersen (1991) highlights the ecological similarities between plants and ants, particularly in the methodology used to investigate their community processes (Harper, 1977).

Ant communities have been described by Hölldobler and Wilson (1990) as being structured by intra- and sometimes interspecific competition in the majority of cases. One way that these phenomena are apparent is in the spatial dispersion of supposedly competing colonies. Regular spatial dispersion is often given as evidence of intra- or interspecific competition between colonies (Bernstein and Gobbel, 1979; Pontin, 1960, 1961) particularly if the nests are more overdispersed than available nest sites (Elmes, 1974). Levings and Traniello (1981) offer a model to explain the mechanism determining spatial distribution, where single species are arranged in hexagonal regularity at their highest densities, and tending towards randomness at lower densities, assuming foraging radii of the same magnitude and unrestricted nest sites. Availability of nest sites and low colony density cause patterns tending towards randomness, and relative strengths of intra- and interspecific competition alter the degree to which nearest neighbour identities are predictable: if negative intraspecific interactions are of greater strength than interspecific interactions, then nearest neighbours are predictably members of other species. If the magnitudes of these interations are equal, there is no pattern in nearest neighbour identity. Savolainen and Vepsäläinen (1988) and Pontin (1960) showed that spatial patterns can be caused by intra- or interspecific behavioural interactions.

Ants have several strategies for spacing colonies regularly: queens attempting to found new colonies may be killed by conspecific workers of other colonies (Pontin, 1960), or incipient colonies may be attacked (Wilson, 1971). Nests may be relocated (Smallwood and Culver, 1979), or adult mature colonies may fight to the death as in *Camponotus gigas* in Brunei (personal observations).

In Australia, a patchwork of colonies of territorially exclusive *Iridomyrmex* species is interspersed with more submissive *Camponotus* colonies and other submissive species (Greenslade, 1979). A similar situation exists between a dominant and a more submissive *Formica* species in Finland (Savolainen et al., 1989). This spatial 'mosaic' phenomenon is documented in several ant communities. Leston (1973), Majer (1976a,1976b,1976c), Room (1971) and Jackson (1984) studied arboreal ant mosaics in Africa. Room found ten dominant species out of 128 species, five of which he investigated in detail. He assembled for each species sub-communities of positively associated ant species and other arthropod species. These dominant species and sub-communities are arranged in a mosaic fashion throughout the cocoa canopy. (Majer, 1972) also found that eight species in Ghanaian cocoa farms were mutually exclusive. Majer (1976b, 1976c) proposed that nesting sites, insolation and homopteran bugs (from which the ants drink honeydew) influence the distribution of dominant ant colonies. Room (1971) noted that successional stage of vegetation is important in determining dominant ant distributions in more detail. Jackson (1984) found differences in the level of spatial exclusion between species colonies nesting at ground level and in the vegetation layer: interspecific overdispersion of colonies was found only in arboreal fauna: she proposed that lower species richness and richer food resources in the canopy are related causally in some way to this phenomenon. Majer and Camer-Pesci (1991) examined the ant mosaic in Australian native ecosystems and tree crops, and found an overdispersed pattern of *Oecophylla* interspersed with nests of a *Crematogaster* species, a similar situation to that found in all the African cocoa farm studies. Leston (1978) examined the mosaic in the Neotropics and Majer (1993) reviewed and compared the mosaics in the New World, Old World and Australian fauna, finding similar patterns worldwide. Levings and Franks (1982) examined the concept of overdispersion in the ground nesting ant community of a New World tropical rain forest, and claimed to find significant evidence of inter- and intraspecific overdispersion. Briese and Macauley (1977) proposed that for ants in semi-arid Australia, spatial arrangements result mainly from behavioural interactions determined by intrinsic properties of the individual species, and are little affected by vegetational differences between habitats, but Bernstein and Gobbel (1979) showed that distributions of ant colonies in North American deserts are notably affected by vegetation structure which alters shading, and hence suitable nest sites, between elevations and show evidence of interspecific overdispersion only at elevations with less vegetation. Vegetation architecture, loose wood (nest sites) and epigaeic fauna influence community structure in Finnish sand dunes (Gallé, 1990, 1991): Doncaster (1981) found that lack of nest sites on Ramsey Island, Wales, resulted in a clumped distribution of nests. Thus the spatial effects of behavioural processes can be ameliorated by envrionmental or other factors.

This study addresses the following questions: What are the patterns of colony dispersion at the community, subfamily and species levels? Specifically: is there evidence of overdispersion amongst colonies, implying competition sensu Levings and Franks (1982), and are the identities of nearest neighbours other than that expected by chance? I suggest possible reasons for the resulting patterns, in the light of evidence for competition, biology of the species and availability of nest sites.

Spatial analyses of the type frequently used in studies on ant colony dispersion, namely nearest neighbour analyses, are subject to certain biases, caused by edge effects (Donnelly, 1978; Sinclair, 1985). I have reanalysed the data on distributions of two subfamilies of ants on the forest floor in Panamanian tropical rain forest (Levings and Franks, 1982), and show that claims for significant overdispersion of colonies at the community and subfamily levels no longer hold when the necessary correction factor is used in the spatial analysis, and that in any case, spatial distributions of any type cannot directly be attributed to any particular type of competition without more detailed knowledge of the species density, biology, behaviour and colony structure.

Methods

FIELDWORK

The fieldwork was carried out in two 10x10m plots on the West Ridge of the Sungai Belalong, which were about 50m apart from each other. The plots were slightly sloping, but as flat and homogeneous as possible (average slope 5 degrees). Each plot was demarcated with string and markers and the surface of the ground cleared of leaf litter and twigs, in order to facilitate following ants and locating their colony entrances, which is not possible if litter is present. Large pieces of dead wood (>10cm diameter) were left in situ, as they are often partial nest sites for ground dwelling species and did not interfere with location of species' colonies. The plot was marked out further into 1x1m squares. Each 2x2m area was baited with mashed sardine on pieces of paper which were laid out in a grid at 30cm intervals. The ants responding to the baits were followed back to their nest entrances and these marked with numbered flags and the coordinates recorded. Specimens of the inhabitant ants were collected and preserved for later identification. The colonies of any other ground and dead wood dwelling ants active in the area were also mapped. Only ants responding to the baits or those found active during the study period were recorded, thus eliminating other ecological groups, nocturnal and non responsive species from the study. The census was continued until no more colonies were found in several hours of search on two consecutive days. The baits were moved around in order to attract foragers from every possible colony. The census of each plot by one person took about 40 hours. The method implemented parallelled that used by Levings and Franks (1982), with which the results were compared.

Assumptions used in the method include that the major nest entrances were independent of each other, i.e. each entrance represented a different colony. This is a possible major source of error. Marking individuals of the commonest species, *Odontoponera transversa*, in order to ascertain colony membership, proved prohibitively labour intensive and time consuming and did not clearly illustrate the colony structure, because the loyalty of individuals to particular nest entrances of the same nest, as in *Lasius neoniger* (Traniello and Levings, 1986), could not be ruled out. Excavation of *O. transversa* nests proved impossible. Inspection of maps of the species' nest entrances did not reveal clearly demarcated clumps of nest entrances identifiable as separate colonies.

Krzysztof Roscisziewski (pers. comm.) has reported the same problems with the species at Pasoh, Malaysia.

I viewed the nest entrances as points in space in the same way as Levings and Franks (1982). Plots were as homogeneous as possible and assumed to be so, and colonies were assumed to be stationary throughout the study.

The patterns of nest dispersion were examined for the community of three subfamilies only: the Myrmicinae (small to tiny generalists), the Ponerinae (primarily medium to large generalists and also specialist hunters) and the Dolichoderinae (one species only, *Lowriella boltoni*, a small generalist).

ANALYSIS

Investigation 1: Dispersion of nests

Are nest entrances of ant species on the forest floor dispersed randomly? The Clark and Evans (1954) nearest neighbour test of spatial dispersion was used to look at the dispersion patterns of all nest entrances, for each of the three subfamilies and for species with 12 or more entrances in each study area. The index of aggregation, R, is given by:

$$R = \frac{\bar{r}_A}{\bar{r}_E} \qquad \text{(eq. 3.1)}$$

where $\bar{r}_A$ is the mean distance to nearest neighbour:

$$\bar{r}_A = \sum \frac{r_i}{n} \qquad \text{(eq. 3.2)}$$

and r_i = measured distance to nearest neighbour for individual i, n = number of individuals in the study area and $\bar{r}_E$ = mean expected distance to nearest neighbour

$$\bar{r}_E = \frac{1}{2\sqrt{\rho}} \qquad \text{(eq. 3.3)}$$

where ρ = density of organisms:

$$\rho = n/\text{size of study area} \qquad \text{(eq. 3.4)}$$

The index varies from $R = 0$ (perfectly clumped), $R = 1$ (random), to an upper limit of around 2.15 for perfect hexagonal regularity.

The statistical sigificance of R may be tested as follows:

$$Z = \frac{\bar{r}_A - \bar{r}_E}{S_r} \qquad \text{(eq. 3.5)}$$

where Z = standard normal deviate and S_r = standard error of $\bar{r}_E$:

$$S_r = \frac{0.26136}{\sqrt{n\rho}} \qquad \text{(eq. 3.6)}$$

As this test is unbiased only when a boundary strip or correction factor is included in the analysis, each analysis was performed on the data set using the

Donnelly (1978) correction of the Clark and Evans test: (Sinclair, 1985) noted the validity and power of the Donnelly correction factor, and that the magnitude of bias of the Clark and Evans test has not been appreciated by those implementing the test in the past (see investigation 3).

The correction is made as follows:
$\bar{r}_c$ = expected distance to nearest neighbour corrected for lack of a boundary strip:

$$\bar{r}_c = \bar{r}_E + \left(0.051 + 0.041 \big/ \sqrt{n}\right)\left(L/n\right) \quad \text{(eq. 3.7)}$$

where L = length of the boundary of the whole study area.
The standard error of the expected distance, S_r, is:

$$S_r = \frac{\sqrt{0.07A + 0.037L\sqrt{A/n}}}{n} \quad \text{(eq. 3.8)}$$

where A = area of study.

These corrected values are used in the index of aggregation equation in the same way as in the Clark and Evans test.

Investigation 2: Identity of nearest neighbours

Is the identity of the nearest neighbour of a nest dependent on the identity of the nest? The data were analysed using a G-test of independence with Williams correction (Sokal and Rohlf, 1969). The data points included in the analysis are only those where the nearest neighbour distance of the nest is smaller than the minimum distance from the nest to the edge of the plot, so that in cases where the certainty of the nearest neighbour being within the plot is not complete, the nest is excluded from the analysis.

Investigation 3: Reanalysis of Levings and Franks (1982)

Levings and Franks (1982) claimed to show that nest entrances of ant colonies on the floor of Barro Colorado Island forest in Panama were regularly dispersed. Their analysis, using the nearest neighbour test, showed significant or highly significant overdispersion in all four cases where all members of two subfamilies were considered, but they did not use a boundary area or correction factor to remove bias at the edge of the plot. I have reanalysed their data, without and then with the Donnelly correction factor. The data were gleaned from maps in the original paper using data retrieval software on a power Macintosh with a 16x16 inch screen.

Results

Investigation 1: Dispersion of nests

Figs 3.1 and 3.2 show the maps of ant colony nest entrances in Bruneian plots 1 and 2.

Fig. 3.1: Map of ant colony nest entrances in plot 1.

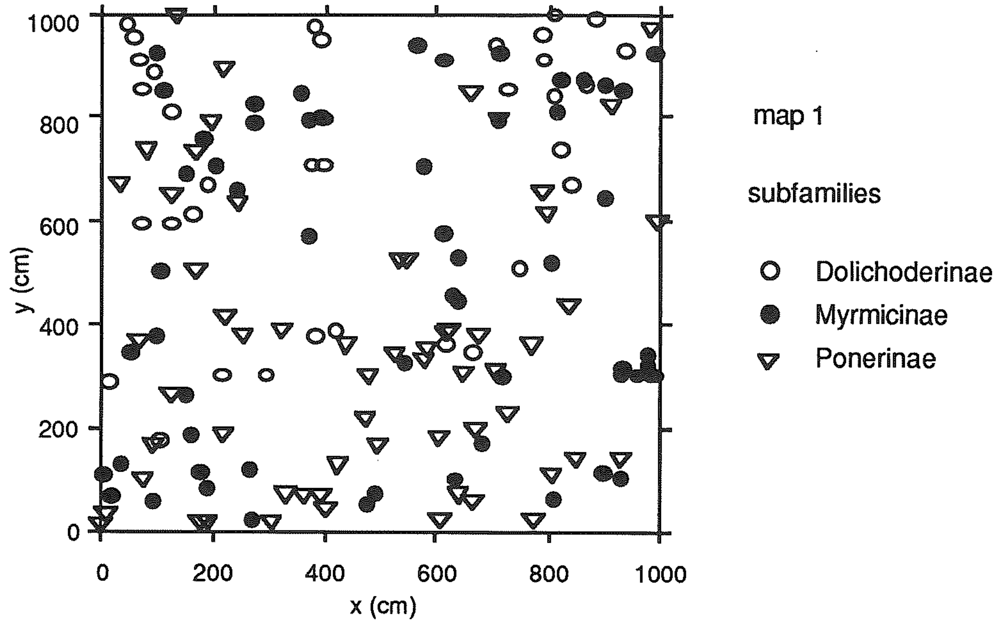
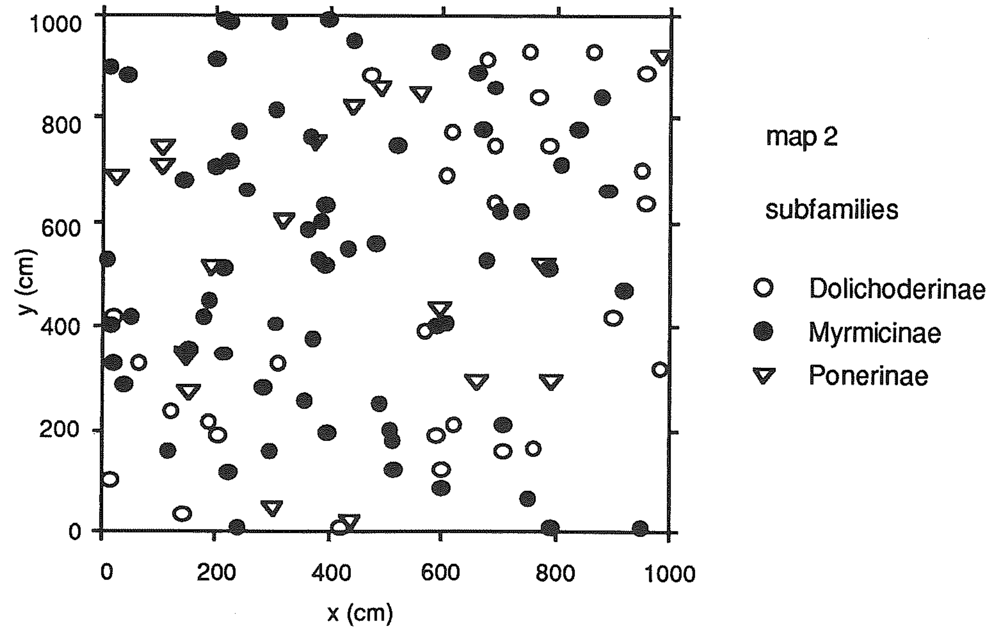


Fig. 3.2: Map of ant colonies in plot 2.



The numbers of nest entrances, nest sites and foraging ranges of the species involved in the study are listed in table 3.1.

Table 3.1: The species found in plots 1 and 2 and their nest sites, foraging ranges and number of nest entrances in plots 1 and 2. d = dead wood, g = ground, l = litter, v = vegetation

Species	Species number	Nest site	Foraging range	Number of nest entrances	
				plot 1	plot 2
subfamily Dolichoderinae					
Lowriella boltoni	151	g	l	37	30
subfamily Myrmicinae					
Calyptomyrmex sp.1	114	d and g	l	2	0
Lophomyrmex bedoti	181	d and g	l	3	29
Monomorium sp.3	192	d and g	l and v	0	2
Myrmecina sp.1*	107	g	l	3	0
Oligomyrmex	300	d and g	l and v	1	0
Pheidole group a	204-216	d and g	l	16	13
Pheidole sp.b7*	239	d (?) and g	?	2	0
Pheidole sp.c1	223	g	l and v	4	2
Pheidole sp.e1	227	g	l and v	12	12
Pheidole sp.e3	225	g	l	0	1
Pheidole sp.e8	230	g	l	0	1
Pheidologeton sp.2	185	d, g and v	l	5	0
Proatta sp.1	187	d and g	l	0	2
Recurvidris sp.2	189	d and g	l	1	0
Tetramorium sp.1	88	d and g	l	2	0
Tetramorium sp.7	94	d and g	l	1	1
Tetramorium sp.11*	98	g	l	0	2
Tetramorium sp.12	99	g	l	4	0
Vollenhovia sp.2*	105	d (?) and g	?	1	0
subfamily Ponerinae					
Cerapachys sp.5*	124	g	l and g	4	0
Diacamma intricatum	3	g, beneath saplings	l and v	1	0
Gnamptogenys sp.3	127	d (?) and g	l	0	1
Hypoponera sp.3	132	d and g	l	1	0
Hypoponera sp.4	133	d and g	l	1	0
Hypoponera sp.5*	134	d and g	l	1	0
Leptogenys diminuta	141	g	l	15	1
Odontoponera transversa	3	g	l	29	11
Pachycondyla astuta	150	g	l	1	0
Pachycondyla sp.6*	151	g	l	5	3

* found only in this investigation and with no other sampling methods.

Further details of foraging behaviour of some species can be found in chapter 4. The results of nearest neighbour analyses on subfamilies and more numerous species are in tables 3.2 and 3.3.

Tables 3.2 and 3.3: Results of nearest neighbour analyses of nest entrance distributions for plots 1 and 2 respectively.[1]

Plot 1	Donnelly's correction			
	entrance number	R	Z	probability
whole community	158	0.98	-0.34	NS
Lowriella	37	0.66	-3.65	<0.001
Myrmicinae	59	0.88	-1.64	NS
Ponerinae	62	0.94	-0.84	NS
Pheidole sp.e1	12	0.84	-0.95	NS
Leptogenys 6	15	0.83	-1.10	NS
Odontoponera transversa	34	1.13	1.35	NS

Plot 2	Donnelly's correction			
	entrance number	R	Z	probability
whole community	115	1.03	0.51	NS
Lowriella	30	0.96	-0.37	NS
Myrmicinae	66	0.98	-0.35	NS
Ponerinae	19	0.90	-0.77	NS
Pheidole sp.e1	12	0.94	-0.35	NS
Lophomyrmex bedoti	29	0.87	-1.22	NS
Odontoponera transversa	13	0.66	-2.08	<0.05

These results show from corrected values that there is significant non-random dispersion of *O. transversa* in plot 2, and *Lowriella boltoni* in plot 1: both are significantly clumped. The sample size and significance of clumping of *L. boltoni* are both large: Thus the null hypothesis is accepted for the subfamilies, but it is not necessarily a sufficient decsription for the individual species.

Investigation 2: Identity of nearest neighbours

Tables 3.4 and 3.5 show the results of a G-test analysis of dependency of identity of nearest neighbours at the subfamily level for plots 1 and 2 respectively: in plot 2 the subfamilies Dolichoderinae and Ponerinae were combined in the analysis, as expected values were less than 5 in more than 20% of cases (Zar, 1984).

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[1] NS = not significant at the 0.05 level unless otherwise stated

Tables 3.4 and 3.5: Results of G-tests of contingency with Williams correction on the identity of nearest neighbours at the subfamiy level.

Plot 1	Dolichoderinae	Myrmicinae	Ponerinae
Dolichoderinae	20	6	4
Myrmicinae	10	23	11
Ponerinae	8	15	26
	G	30.05	
	p	<0.005	

Plot 2	Dolichoderinae and Ponerinae	Myrmicinae
Dolichoderinae and Ponerinae	17	17
Myrmicinae	19	27
	G	0.59
	p	NS

There is highly significant dependence of the identities of nest and nearest neighbour in plot 1, where the null hypothesis is rejected. Comparison of the results for plot 1 with expected values (table 3.6) show that in all 3 subfamilies, there are markedly higher observed than expected numbers of nests with nearest neighbours of the same subfamily.

Table 3.6: Expected values for numbers of nearest neighbours of three subfamilies in plot 1.

Plot 1	Dolichoderinae	Myrmicinae	Ponerinae
Dolichoderinae	**9.27**	10.73	10.00
Myrmicinae	13.59	**15.73**	14.67
Ponerinae	15.14	17.53	**16.33**

G-tests were performed on the data collapsed around cells of interest in order to ascertain the significance of individual interactions, for the three subfamilies in plot 1. The results of these are in table 3.7.

Table 3.7: Results of G-tests with Williams correction on dependence of identity of nearest neighbours collapsed around three subfamilies, in plot 1.

subfamilies	G	p	pattern
Dolichoderinae and others	21.76	<0.005	neighbours the same
Myrmicinae and others	7.81	<0.01	neighbours the same
Ponerinae and others	13.87	<0.005	neighbours the same

The same test was used on data for species of sufficient abundance (i.e. where expected values were not below 5 in more than 20% of cases: Zar, 1984) in the study area, with other species in their subfamily. Results for *O. transversa* and *Lophomyrmex bedoti* are in tables 3.8 and 3.9 respectively. Expected results for *L. bedoti* are in table 3.10.

Tables 3.8 and 3.9: Results of G-tests with Williams' correction on the identities of nearest neighbours at the species level.

Plot 1	*Odontoponera transversa*	other Ponerinae
Odontoponera transversa	16	9
other Ponerinae	8	13
	G p	3.00 NS

Plot 2	*Lophomyrmex bedoti*	other Myrmicinae
Lophomyrmex bedoti	16	8
other Myrmicinae	6	20
	G p	9.65 <0.005

Table 3.10: Expected values of identities of nearest neighbours for *L. bedoti* in plot 2.

Plot 2	*Lophomyrmex bedoti*	other Myrmicinae
Lophomyrmex bedoti	10.56	13.44
other Myrmicinae	1.44	14.56

These results show significant evidence for dependence of colonies and their neighbour's species identities in the case of *L. bedoti* in plot 2. The species is more likely to be located closest to one of its own species.

Investigation 3: Reanalysis of Levings and Franks (1982)

The results of the reanalysis for all nests are in table 3.11, and for the subfamlies are in table 3.12. Levings and Franks own values of R and p-values are given, followed by my own analysis of the data without and then with the correction factor.

Table 3.11: Results of reanalysis of nest distribution data of Levings and Franks (1982), for all nests.

plot	Levings R	Levings probability	R	probability	corrected R	corrected probability
a1	1.18	<0.05	1.2	<0.05	1.12	NS
a2	1.11	<0.05	1.16	<0.01	1.11	NS
a3	1.27	<0.001	1.27	<0.001	1.19	<0.05
a4	1.12	<0.05	1.15	<0.05	1.09	NS

These results clearly show that the bias caused by the lack of a boundary area or correction factor in the original anlaysis of Levings and Franks (1982) has led to a spurious finding of overdispersion. We cannot therefore reject the null hypothesis that the distribtion of all nests on the floor of the forest on Barro Colorado Island is random.

Table 3.12 shows the results of reanalysis of the data for individual subfamilies.

Table 3.12: Results of reanalysis of nest distribution data of Levings and Franks (1982), for 2 subfamilies.

plot and subfamily	Levings R	Levings probability	R	probability	corrected R	corrected probability
a1, Ponerinae	1.22	<0.05	1.19	<0.05	1.10	NS
a1, Myrmicinae	0.80	NS	0.85	NS	0.72	NS
a2, Ponerinae	1.14	<0.05	1.19	<0.01*	1.13	NS
a2, Myrmicinae	0.79	NS	0.98	NS	0.90	NS
a3, Ponerinae	1.33	<0.01	1.23	NS*	1.10	NS
a3, Myrmicinae	1.20	<0.001	1.23	<0.05*	1.13	NS
a4, Ponerinae	1.16	<0.05	1.18	NS*	1.09	NS
a4, Myrmicinae	1.22	<0.01	1.23	<0.01	1.14**	NS

These results show that we can not reject the null hypothesis that nests of ants of the subfamilies Ponerinae or Myrmicinae are dispersed at random on the island. In cases where my uncorrected reanalysis values of R and probability do not agree with Levings and Franks (1982) (disagreeing probabilities are starred), it is possible that the data gleaning process was not accurate enough, or that the map was not a sufficiently accurate representation of the data. The equivalent values of R (**) in Levings' and my analyses with different p-values are probably due to the corrected standard error giving a different Z-value in my calculation (equation 3.8).

Discussion

In contrast to the original findings of Levings and Franks (1982), no evidence of overdispersion was found amongst ant colony nest entrances in plots 1 or 2 in Bruneian rain forest, or in 4 plots in Panama, at the community or subfamily levels. Although not significant, most of the analyses in the Bruneian study tend towards clumped dispersions, and those in the Panamanian study towards regular dispersion. In the Bruneian plots, the most significant results were found in plot 1. This could have been predicted from the models of Levings and Traniello (1981) and Ryti and Case (1992, see below).

In one Bruneian plot, *Lowriella boltoni* was found to be significantly clumped, as was *Odontoponera transversa.* in the other. There was significant dependence of identity of nearest neighbours of all subfamilies in the Bruneian plot 1, and of *Lophomyrmex bedoti* and other Myrmicinae in plot 2, where nearest neighbours were significantly more likely to be of the same subfamily in the former case, or species in the latter.

Ryti and Case (1992) made a simulation model of neighbourhood competition, comparing its predictions with empirical data on ant spatial distribution. They found that competition can result in many spatial arrangements, not just overdispersion, and that overdispersion is most readily evidenced by mortality of young colonies that settle near established conspecifics. In cases where competition occurs between established colonies, nest dispersion is random. In the former case, spacing increases in regularity as density of colonies increases. Competition can result in random or clumped spatial arrangements in the following way: intraspecific clumping may result from high interspecific competition relative to intraspecific competition, high colony death rates or turnover (r-selection) and low intraspecific colony density. Adult/ adult colony attack in negative intraspecific colony interactions always results in a more random intraspecific dispersion than adult/ juvenile colony or founding queen attack. The identity of nearest neighbour colonies varies with the relative strengths of intra-/ interspecific competition: the nearest neighbour will be conspecific if interspecific competition is stronger, and heterospecific if intraspecific competition is stronger. It is not known, however, which of these situations is correct in this case. It is possible, for example, that the enormous diversity of species in this habitat leads to higher inter- than intraspecific competition, and this has resulted in random or clumped intraspecific colony distributions. Unicolonial species are also likely to be subject to higher inter- than intraspecific competition, as they do not show aggression intraspecifically (Hölldobler, 1990). High species turnover is also most likely in the litter/ ground fauna than anywhere else: the species often live in at least partially ephemeral nest sites which are easily disturbed (unlike tree holes or large logs) by *Leptogenys* for example, and I have noticed that reproductives attracted to lights at night are usually of litter and/ or ground dwelling species.

The possibility that the nest entrances were not independent must be considered. Little is known about the biology of *Odontoponera transversa*: it is possible that it is unicolonial, with multiple nest entrances, as are many opportunist and 'tramp' species (Williams, 1994). I have found this species in habitats from primary rainforest to grassland all over South East Asia, and aggression tests showed that there is no intercolony aggression of neighbouring nests, or of more distant nests, although its foraging success is reduced in the presence of other species (see chapter 4). If it is unicolonial, it is valid to look at distributions of these entrances with respect to identity of nearest neighbours: Traniello and Levings (1986) found that multiple nest entrances of *Lasius neoniger* were overdispersed to maximise utilisation of foraging space and minimise interspecific interactions. Overdispersion in *L. neoniger* was clearly not due to intraspecific competition, however. It is even conceivable that strong interspecific competition in this species rich habitat has *caused* a colony structure tending towards unicoloniality in some species, such as *O. transversa* and *Lowriella boltoni*, the most likely candidates for multiple nest entrances in this study. Levings and Franks' (1982) include a unicolonial species, *Wasmannia auropunctata*, in their study. They found it the most overdispersed of all species or groups in their study. Bearing in mind the lack of correction factor in their analysis, it is wrong to conclude any kind of intraspecific competition from this finding, as this species shows no aggression when colonies are mixed (Williams, 1994). Intraspecific overdispersion, if it occurs, may have a function other than being the result of intraspecific competition.

There was not sufficient data to test the dispersion patterns or nearest neighbour identities of other individual species, so it is not possible to describe a general pattern for more species.

The greater number of specialised species in the Bruneian study, including small myrmicine species, may have caused a dependence of identity to be found where surface litter agglomerations or other factors made patches of the plot more suitable for some primarily litter dwelling species. Many of the species collected may have more specialised feeding habits, and possibly nest site preferences, than the more generalist species included in Levings' study (see chapters 2 and 4). The significant dependence of identities of nearest neighbours may again be a habitat preference effect (as in *L. bedoti*, discussed above). It is also possible that factors such as the locations of pieces of dead wood on the forest floor may have affected the distribution of partially dead wood dwelling species, such as *Lophomyrmex bedoti*, so that they appear more abundant in certain parts of the plot. Individual species within the subfamily Myrmicinae were not shown to be significantly clumped, suggesting some ecological reason for the dependence of identity that affected many species in the subfamily. It is also possible, however, that type 1 error, as highlighted by Meagher and Burdick (1980), may have ocurred. All nests included as data points in the analysis are not in fact independent, leading to a spurious finding of dependence of the identities of nearest neighbours.

Ryti and Case (1992) found in their simulations that in some types of ant species, greater regularity of dispersion results from higher density. It is possible that at the time of year this study was performed, the species of interest may have not been at highest density. Moister litter may have encouraged some species to nest out of the ground, and these could have been removed from the area with the superficial litter at the start. This may explain the difference in the tendencies of dispersion indices in the two studies. It would have been useful to have recorded litter depth and composition across the plots at the beginning of the study. The effect of tree boles may also have caused the difference in the results of the studies, and as data were not available on this matter, a comparison was not possible. The Bruneian plots were chosen not to have large trees in them, but small ones (diameter breast height <10cm) were common and 2-3 medium sized ones were present in both plots. It was not thought that trees would affect the results of testing for random dispersion in the Brunei study, although preference for nesting at the base of larger trees would result in a clumped distribution. Another factor affecting nest sites may have been slope, although this varied negligibly within and between the Bruneian plots.

If Levings and Traniello (1981) used the uncorrected Clark and Evans method to analyse the nest dispersion of ant species, the results must be treated with great caution. In a review of a large body of data on ant colony distributions, their conclusion after surveying this data, and some reanalysis, was that intraspecific overdispersion, and hence competition, are primary forces in the structuring of ant communities, occurring in the majority of cases studied. As suggested by Sinclair (1985), it should be possible to convert the uncorrected to the corrected significance level directly given experimental variables. Quadrat variance methods (Ludwig and Reynolds, 1988; Krebs, 1989) may be another way to deal with the problems of mapped data outlined above, although comparing results from both methods without corrections, as Levings and Traniello (1981) did, would not be valid. Ryti and Case (1986) also implemented the Clark and Evans test without correction.

As Krebs (1989) notes, the scale of investigation can strongly influence the apparent dispersion of individuals. A given size of study area does not necessarily give a true representation of the dispersion of all species. The original Clark and Evans nearest neighbour test cannot resolve dispersions that occur at different spatial scales, e.g. regularly spaced clumps of regularly spaced nest entrances as in harvester ant communities in American deserts (Ludwig and Reynolds, 1988). Tests that are able to do this include modifications of the test which also use distances to the 2nd-nth nearest neighbours (Krebs, 1989), and the T-square sampling procedure (Ludwig and Reynolds, 1988). Diggle (1976) has reviewed spatial pattern analyses.

It is necessary to define which type of species are involved, relative densities, turnover rate and mode of intra-/ interspecific colony spacing in order to truly infer competition from any spatial distribution. As numbers of species in a study increase, and /or the biology of their interactions becomes less well known, inferring any causal factor, or lack of it, from a spatial pattern becomes more difficult. Competition may be present in species exhibiting a regular, random or clumped distribution. Manipulative field testing is the only way to be sure (Connell, 1983; Schoener, 1983; Keddy, 1987).

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CHAPTER FOUR

Foraging strategies and behavioural interactions in a rain forest ant community

Introduction

The importance of competition and prevalence of dominance hierarchies in ant communities has already been noted, as has the ecological similarity between ant colonies and plants. Rayner and Franks (1987) propose that ants are ecologically and evolutionarily similar to fungi, thoroughly exploiting their local resource environment usng a series of ramifying hyphae, or foraging trails, in which different genetical strains are interdigitated, but avoid each other. Whatever the ecological similarities of ants and other organisms, it remains that ants also have unique and complicated social mechanisms and communication systems that set them apart from other organisms, and enable them to use available resources in ways that most other organisms cannot. Behavioural dominance, recruitment and foraging pattern are all adjustable to the needs of a colony at any given time. These mechanisms have caused the ecological success and numerical dominance of the ants in many of the world's terrestrial biomes (Wilson, 1990). Eusociality has given insects more control over their environment (Janzen, 1977).

It is important at this point to define the term dominant: although a definition was given in chapter one, it should be noted that authors often confuse or combine the meanings of numerical and behavioural dominance (e.g. Leston, 1973b). I use the term at all times in its original sense, as 'ruling or influential', i.e. having a demonstrable negative effect on other species. Numerical dominance is always qualified as such. These issues are discussed by Greenslade (1976).

Many students of behavioural hierarchies in ant communities have noted similar patterns in resource use and interspecific relations among species which are at different levels in the hierarchy: dominant (more aggressive) species tend to monopolise baits, and force more submissive species to forage on less desirable baits and vertical strata or at less favourable or times of day. This improves their own energy input, but can reduce reproductive success of the more submissive species. These patterns were shown to operate in the Finnish Tvärminne archipelago (Savolainen and Vepsäläinen, 1988; Vepsäläinen and

Savolainen, 1990). Vepsäläinen and Pisarski (1982) propose a useful three tiered classification for ants in this habitat

I submissive species - defend only their nests
II encounter species - defend nest and food finds
III territorial species - defend nest and all foraging areas

Encounter species are unable to survive within territories of territorial species, although submissive species survive better there, despite raids by the territorials and their own reduced abundance. Territorial species are very abundant and recruit most effectively to food, dispersing level I and II species from food baits by aggression or encouraging avoidance. Submissive *Formica* species took smaller prey in the presence of dominant *Formica*, and moved from higher quality protein baits to poorer carbohydrate. Vepsäläinen and Savolainen (1990) showed that the presence of dominants reduced the occurrences of submissive *Myrmica* on baits, and suggested a range of ways that the submissive species avoids or minimises confrontation with the dominants: morphological, microhabitat and temporal differences are among these. Similar patterns to these were found in a Scottish heathland ant community (Brian, 1955). The dominant *Formica fusca* was frequently aggressive towards *Myrmica rubra*. The 'peacaeble' *Leptothorax acervorum* was, however, able to coexist with the dominant at baits.

Baits are often used in the experimental investigation of niche relationships and community structure of species (Brian, 1964; Levins et al., 1973; Culver, 1974; Andersen, 1992). They provide a useful and controllable insight into community patterns, particularly in social insects (Colwell and Fuentes, 1975).

Other habitats where hierarchical patterns have been studied in detail include temperate North American woods, and the Australian seasonal tropics. Fellers (1987) was able to almost fully elucidate the hierarchical roles of each of nine species sympatric in a North American temperate forest, by collection of food items to assess resource overlap (which was high), observation and timing of behaviour to quantify negative behavioural interactions, and whether they were aggressive or submissive, and how efficiently each species was able to assimilate the available food resources relative to other species. She examined the roles of two sorts of competition, exploitative and interference, out of the six acknowledged by Schoener (1983), and found an inverse relationship between them. Less aggressive species arrived at baits earlier than other species and exploited as much of the bait as possible before more aggressive species arrived and interfered. Aggressive species also recruited most effectively to baits, i.e. their abundances were higher. Lynch et al. (1980) found in this habitat that the dominant *Prenolepis imparis* more frequently chose protein over carbohydrate food. The reverse was true for the submissive *Paratrechina melanderi.*

Greenslade (1978) and Greenslade and Halliday (1983) described the Australian ant fauna in terms of a 'functional group' classification, based on the taxonomic, ecological and behavioural characteristics of the species which allows the fauna to be divided into seven individual groups. Competitive dominance is a large feature of this classification. *Iridomyrmex*, the meat ants, *Crematogaster* and *Oecophylla* are the dominant genera on this continent. The seven groups may be viewed as 'guilds', sets of species employing similar behavioural and/ or ecological strategies (Terborgh and Robinson, 1986;

Hawkins and Macmahon, 1989). Andersen (1992) described a 'humped' diversity relationship between dominant species (noted above) and others in Australia: as abundances of dominants at baits increased, so too initially did abundances of other species. After a point however, numbers of others fell, as they were repelled by dominants.

In the tropics, such studies are rarer, but Bose and Davidar (1990) used baits to investigate the behavioural competitive hierarchy of ants in the forests of the Western Ghats, India. They found that the aggressive and behaviourally dominant species, *Oecophylla longinoda* and *Crematogaster* spp., occur less together than expected by chance.

Foraging strategies vary enormously in the ants, from the entirely solitary foraging desert genera *Cataglyphis* and *Ocymyrmex*, to the extremely highly organised *Pheidologeton diversus* of Malaysia, with up to ten castes, which practise group retrieval and constructs earthen corridors through which food items are carried by certain castes to the nest.

Hölldobler and Wilson (1990) note the two components of foraging: the search for and retrieval of food items. The ultimate currency of the colony life cycle is energy, and the payoff at colony level selection, output of reproductives. Thus the search for and retrieval of food must input the optimal amount of energy of the correct type to the colony as possible, to maximise payoff. Protein food is favoured by ants in order to produce reproductives and further workers.

Separating the effects of taxonomic and innate behavioural variables, such as recruitment strategies, as explanations for behavioural dominance, is difficult. Workers have variously attributed success of dominant species in interspecific interactions to large body size (Fellers, 1987), small body size (Greenslade, 1971), forager number (Andersen, 1992) and social organisation (Wilson, 1990). Brian (1955) suggests that increased colony size, decreased worker size and increased social organisation have contributed towards ecological success in ant species. The tropical rain forest community offers a large number of species with the greatest possible behavioural and taxonomic variation with which to examine the precise roles of behavioural and taxonomic factors in the structuring of the community. It is possible to ask almost innumerable questions about this complicated system. This study set out to explore the following five areas:

1) Is bait choice dependent on taxonomic group (subfamily) or level of recruitment? I tested for patterns of the type reported by Fellers (1977): Do species which are more efficient recruiters chose higher quality baits, and are less efficient recruiters forced onto poorer food resources? How do the patterns vary from the ground to the trees? Jackson (1984) found that patterns of spatial exclusion of dominant species in African plantations were clearest in the trees.

2) What is the pattern of recruiting strategies in this ant community? Six species with low abundance (recruitment) at baits are tested to establish whether they are solitary foragers, and the magnitude of recruitment in the rest of the community is reported.

3) Is level of recruitment or subfamily correlated with foraging success, as measured by persistence at baits? Do subfamilies differ in their foraging success? How are level of recruitment, persistence and speed to locate baits correlated?

4) Is there variation in the effect of given species on other species presence at baits, or in the effect of other species on given species presence, and is the variation explained by subfamily or level of recruitment? Is there variation in the number of other species occurring with given species at baits, and if so, which behavioural parameter explains it? We would expect species of high level of recruitment to have a stronger negative effect on other species presence and persistence at baits, and on each other compared to the effect on species of lower recruitment ability. How is the foraging success of individual foragers, measured as numbers of times the species accesses and / or takes the bait related to the presence of other species?

5) Is there evidence of a predictable succession of ant species at baits over time? Is the succession based on subfamily or recruitment ability? Do species persist at the bait differentially early or late? Are these patterns related to subfamily or recruitment ability?

I try to simplify the complicated community of 90 bait responsive species into fewer groups which behave and interact in predictable ways. These groups were based on a) subfamily (4 groups) and b) modal abundance scores at baits, interpreted as an index of the level of recruitment (5 groups).

Methods and Results

FIELDWORK

The study took place over a period of five weeks in May, June and July 1993. Each day, I chose a random 10 x 10 m square in the West Ridge hectare using the random number generator on a Casio scientific calculator. Within each square, the co-ordinates for bait points were also chosen randomly. Two plastic feeders were attached to the nearest tree or sapling over 12 feet tall. A large protein bait, consisting of a whole teaspoon of mashed sardine, was placed in one feeder, and a small protein bait of a quarter of a teaspoon of mashed sardine was placed in the other. A carbohydrate bait of half a teaspoon of jam was smeared onto the tree. All three baits were within four inches of each other on the tree trunk. On the ground, within a square meter of the base of the tree trunk, the same types of baits were placed on small pieces of thin white paper. The baits were spaced to give the ants a distinct choice, whilst being far apart enough for me not to confuse the occupants of one bait with another. Hereafter I refer to the baits as noted in table 4.1.

Table 4.1: Codes used throughout the chapter to refer to different baits.

glp = ground large protein
gsp = ground small protein
gc = ground carbohydrate
tlp = tree large protein
tsp = tree small protein
tc = tree carbohydrate

There were eight bait points per square.

I recorded the time at which each bait was set and sampled. After points 1-4 had been set, I returned to the first to sample it. At each point, I noted the species/genera of ants, recorded their abundances on the abundance score scale (see table 4.2 below), noted their foraging success if appropriate (see below), and took specimens of all species I was unable to identify in the field for later identification, which I preserved in 80% ethanol. The bait was topped up between samples to maintain its quality. I was careful to create as little disturbance as possible, and wherever possible, species were only noted. Before I recorded data or collected specimens from each bait, I waited for one minute in order to allow any ants I had disturbed to come to or return to the bait.

Table 4.2: Abundance score scale: I used this scale as an index of recruitment ability of species. It is a modified scale of that used by Andersen (1992).

score	absolute abundance
1	1
2	2-5
3	6-20
4	21-50
5	>50

Figs. 4.1-4.5 show different species found on the baits, at abundance scores from 1-5. After sampling the first four points, the rest were set and sampled. I then sampled all the points in turn for the next four hours, unless observations were cut short by early rain. The study was entirely diurnal.

Preserved specimens were pinned and labelled, and identified to morphospecies (or morphospecies groups in the case of the tiniest *Pheidole sp.* and *Oligomyrmex,* where morphospecies identification was not possible).

ANALYSES

The modal abundance score

The modal abundance score was used to classify the ant community into up to five different groups, depending on the level of recruitment of each species. For each species, the modal value of all the abundance scores of the species on each one of the six bait types was calculated. This was regarded as a statistically robust descriptor of the foraging recruitment strategy of the commoner species, and may be used as a 'foraging recruitment index' at baits.

Different measures of species abundance have been used in the analyses. In non-parametric analyses, species are grouped according to their modal abundance score, i.e. 1-5 (see above) on individual baits. In parametric analyses, the mean abundance score is used. Mean abundance was calculated as the mean of all abundance scores on that bait type. It is approximately valid to take the mean abundance score as it is a simple transformation of the absolute abundance, close to the square root of the absolute value, and its ease of use allows a versatile experimental approach.

Fig 4.1: *Diacamma intricatum*, sp. 2, a solitary forager

Fig 4.2: *Polyrhachis bihamata*, sp. 40, a recruiting species, at abundance score 2

Fig 4.3: Large *Pheidole*, sp. ?, at abundance score 3

Fig 4.4: *Philidris*, sp. 54, at abundance score 4

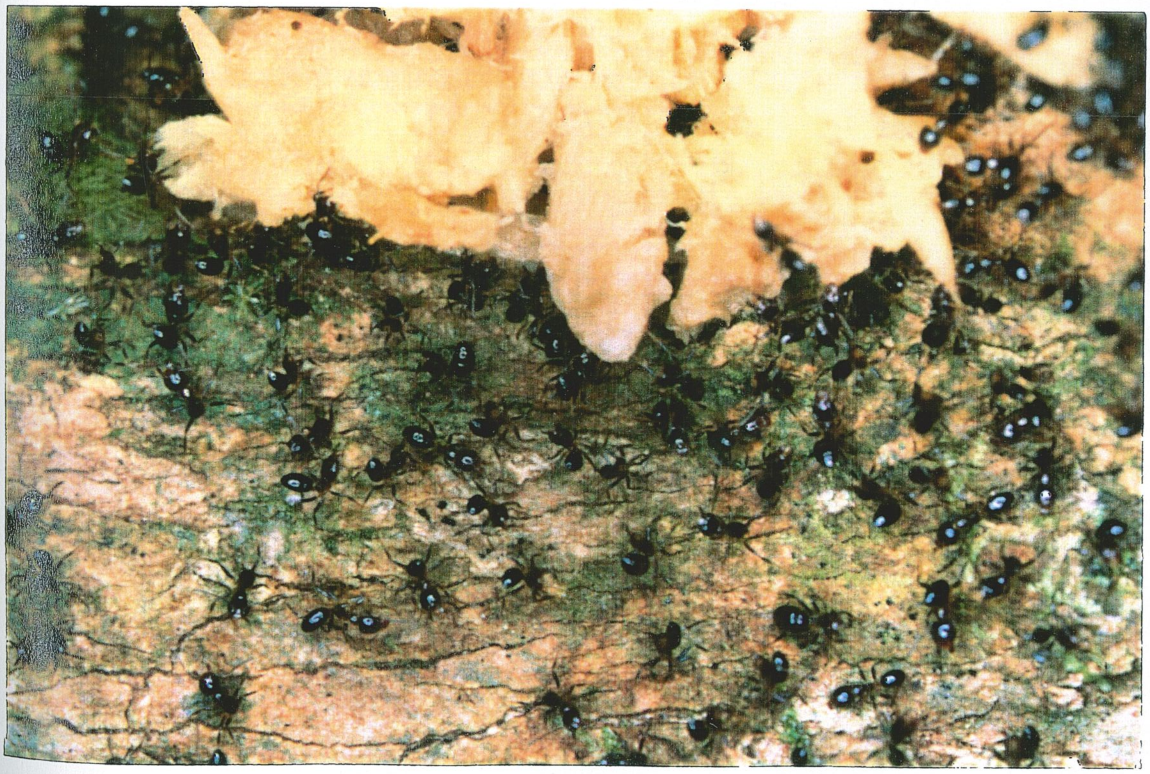


Fig 4.5: *Crematogaster difformis*, sp. 180, at abundance score 5

Investigation 1: Patterns at baits

ANALYSIS

a)Does a species' bait choice depend on its taxonomic group or modal abundance score?

The baits I offered differed in quality, e.g protein is superior to carbohydrate and large protein to small protein (Savolainen and Vepsäläinen, 1988; Fellers, 1987). The number of occurrences of species on different baits might depend on their subfamily, or on their abundance, and bait choice might depend on the vertical level (tree or ground). I therefore used G-tests of contingency to look at inter-dependence between the following bait, abundance and subfamily variables: modal abundance score (1-5), subfamily (Dolichoderinae, Formicinae, Myrmicinae and Ponerinae), tree/ ground baits, and bait type (large protein, small protein or carbohydrate).

b) Do different baits affect the composition of the fauna they attract, or is the difference simply in the modal abundance of the responding species?

As modal abundance scores were calculated for each bait separately, and modal abundance score was found to be dependent on bait type, abundance at baits might differ because the species composition is different or because the same species have different abundance on different baits.

i) I performed a G-test of contingency to test whether numbers of species occurring in modal abundance score groups 1-2 and 3-5 on glp or tlp, and common to all three baits at that level, differ from expectation on other baits at that level. In these and later contingency tests, modal abundance score groups were sometimes combined due to small sample size.

ii) I performed sign tests to test whether baits differ systematically in the abundances attained there by species. The signs of differences of modal abundance score between pairs of baits were calculated and analysed using the sign test.

RESULTS

a) Modal abundance score of species on large protein baits, on tree baits and in the subfamilies Dolichoderinae and Myrmicinae are significantly higher (Table 4.3).

The significant difference among subfamilies in their modal abundance scores is illustrated in figs. 4.6, 4.7 and 4.8.

Table 4.3: Results of G-tests of contingency with Williams' correction on the dependence of abundance, subfamily, bait type and location variables, with patterns found.

Interaction	G	p	pattern
subfamily/ vertical level	<7.82	NS	
subfamily/ bait	<12.59	NS	
subfamily/ abundance	24.79	<0.005	More species of abundance score 3-5 in Dolichoderinae and Myrmicinae. More of 1-2 in Formicinae and Ponerinae
bait/ vertical level	<5.99	NS	
abundance/ vertical level	21.34	<0.005	More abundance score 3-5 species on trees. More 1-2 on ground
abundance/ bait	23.50	<0.005	More abundance score 3-5 species on large protein. More 1-2 on carbohydrate

Fig 4.6: The modal abundance scores of 4 subfamilies on glp. f = Formicinae; d = Dolichoderinae; p = Ponerinae; m = Myrmicinae

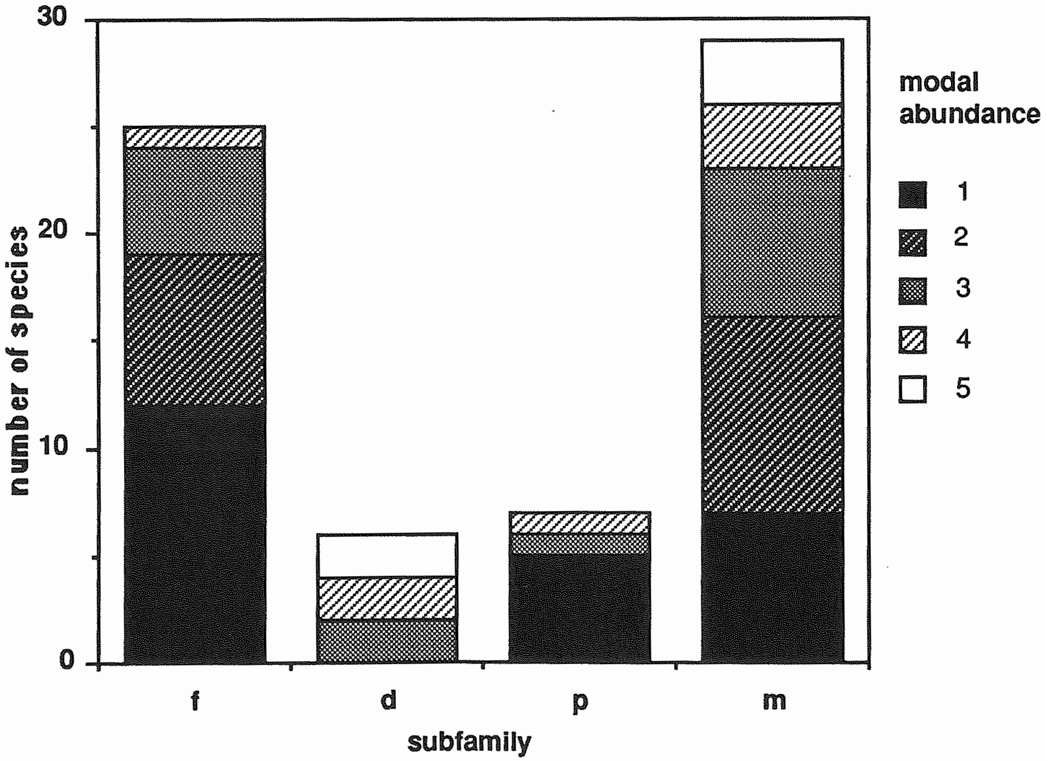
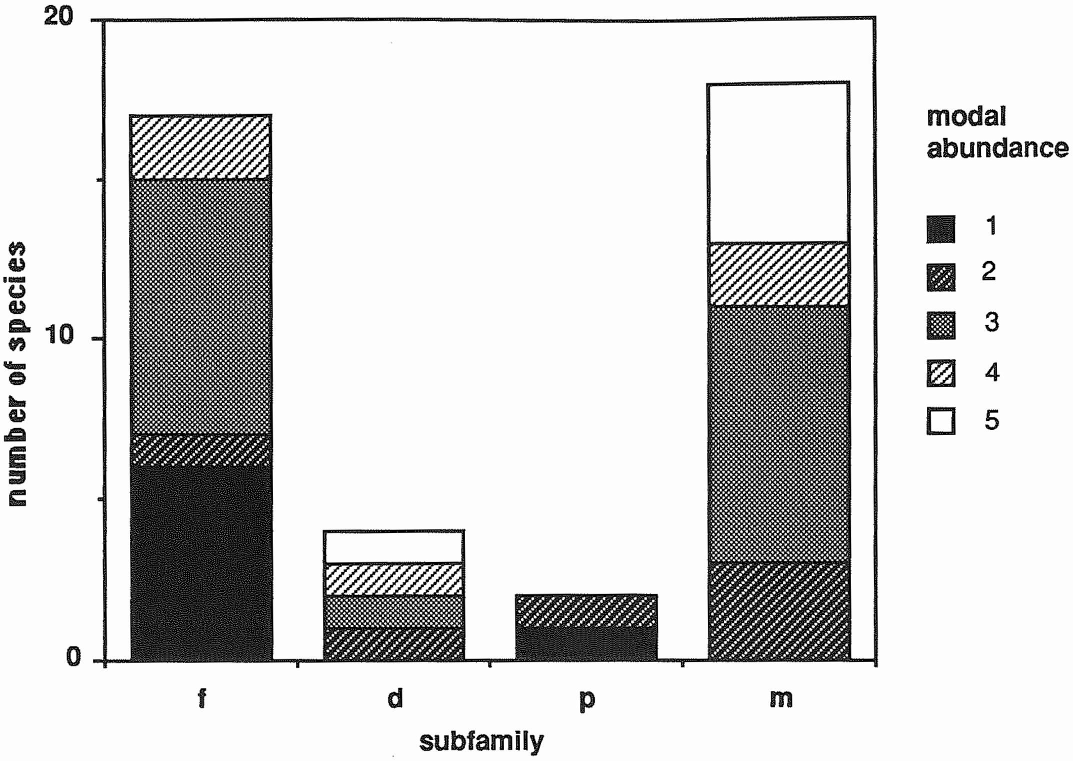


Fig 4.7: The modal abundance scores of 4 subfamilies on tlp. f = Formicinae; d = Dolichoderinae; p = Ponerinae; m = Myrmicinae



b) i) Table 4.4 shows that there is no preference of species of high or low modal abundance score on glp or tlp for particular baits on the ground or trees. Thus potentially dominant species do not occur disproportionately on higher quality baits.

Table 4.4: The results of G-tests of contingency on numbers of species occurring in modal abundance score groups 1-2 and 3-5 on glp or tlp, and common to all three baits at that level, on three bait types at each level.

bait	G	degrees freedom	p
glp	3.54	2	NS
tlp	4.40	2	NS

ii) The results of sign tests on the change in modal abundance score show that modal abundance score of species changes significantly among baits in 3 cases of the eight pairwise comparisons (table 4.5).

In combination, the above results show that differing bait quality does not affect the sort of species that occur on baits, in terms of their modal abundance score on the highest quality bait, but that a species' modal abundance score will change between baits.

Fig 4.8: The modal abundance scores of 4 subfamilies on gc. f = Formicinae; d = Dolichoderinae; p = Ponerinae; m = Myrmicinae

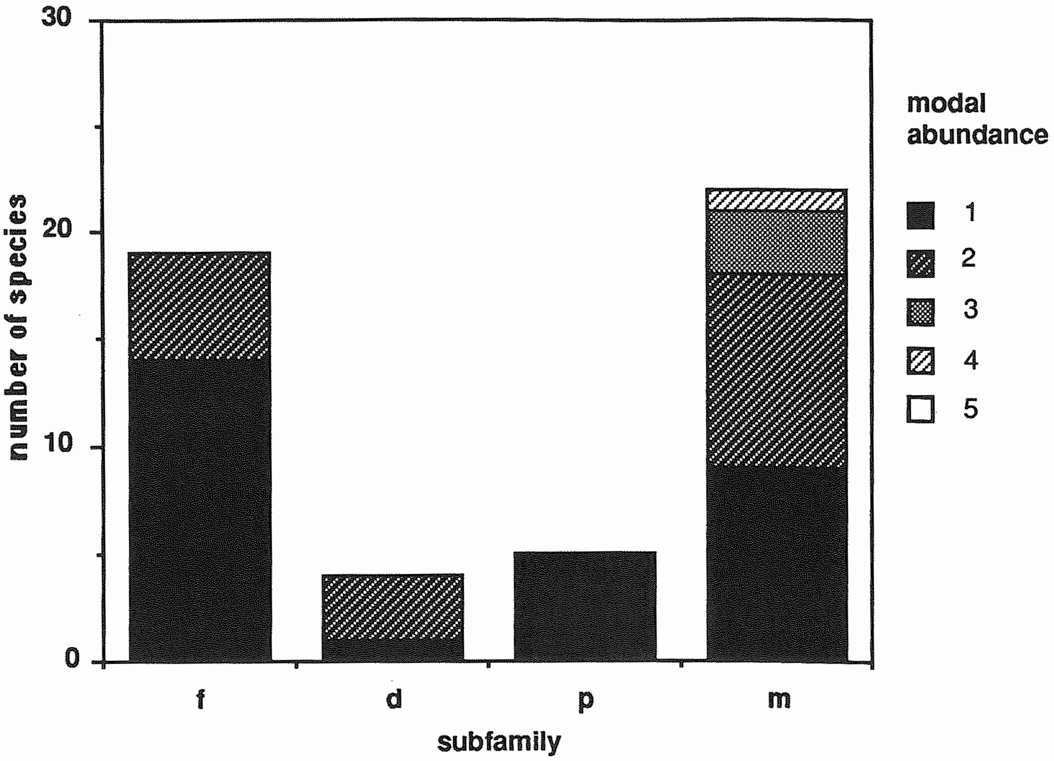
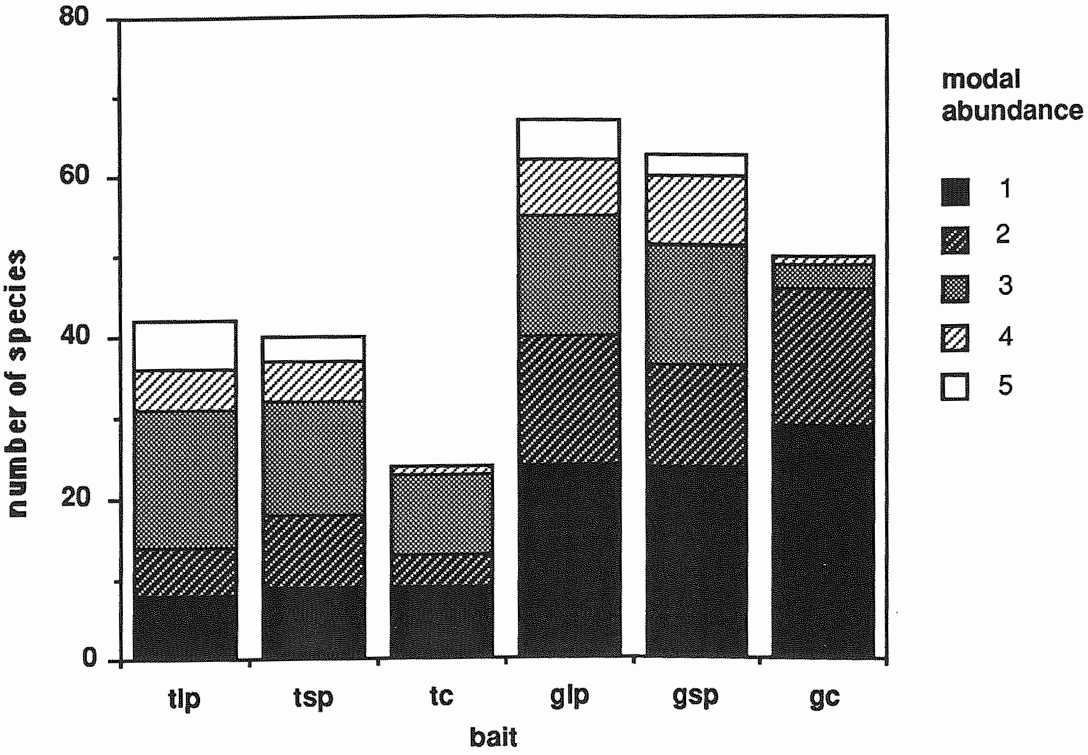


Table 4.5: The results of sign tests on the change in modal abundance score of species from one bait to another on 8 pairs of bait combinations

baits	p	pattern
glp/ gsp	<0.05	abundance decreases glp →gsp
glp/ gc	NS	
glp/ tlp	NS	
gc/ gsp	<0.05	abundance decreases gsp →gc
tc/ gc	<0.05	abundance decreases tc →gc
tc/ tlp	NS	
tsp/ tlp	NS	
tc/ tsp	NS	

Fig.4.9 shows that tree baits and large protein baits attract more species of higher modal abundance, but more species overall are attracted to ground baits.

Fig 4.9: The relative numbers of different modal abundance scores on different baits



Further analyses are for the bait glp unless otherwise stated, as this had the greatest number of occurrences of ants, and bait types showed no qualitative differences in species' subfamily.

Investigation 2: What is the pattern of recruiting strategies in this ant community?

ANALYSIS

a) Which species are solitary foragers?

Some species in the community may be solitary foragers, i.e. they do not recruit nestmates to food finds. These species can be identified as follows: if we take a set of independent samples, then if coocurrences are random, the probability of seeing x individuals on a bait together, and consequently the number of points where x individuals will be seen, can be predicted by the Poisson distribution (Zar, 1984), given the mean abundance.

Independence was achieved by using the abundance scores from all points for the the time intervals 1-30 and 121-150 minutes in separate analyses to ensure that changes in behaviour over time were accounted for.

Mean abundances were calculated by taking a representative absolute abundance value of the abundance scores. These were 1 for abundance score 1, 4 for abundance score 2, and 15 for abundance score 3. These were multiplied by the number of points at which that abundance was seen, and divided by the total number of points of occurrence.

The predicted Poisson probabilities of 0, 1 and 2 or more ants occurring at points were found, the predicted number of points of occurrence of 0, 1 and 2 or more ants calculated, and these compared with the observed values using a

G-test of goodness of fit with Williams' correction. A value of 1 was added to values used in the G-test due to small values.

b) What is the pattern of foraging in other species?

The number of occurrences at points, mean and modal abundance scores of all species found on baits can be seen in appendix 4.

RESULTS

a) Table 4.6 shows that in all cases except *D. intricatum* at 121-150 minutes, the null hypothesis cannot be rejected, and there is no evidence to suggest that the ants occur in abundances other than what would be expected randomly. *O. transversa* occurs in abundance of 2 significantly less than expected, implying some avoidance of individuals, and possibly intra-specific competition. As *D. intricatum* occurs much more frequently in the first 30 minutes of bait availability than at other times (18 occurrences at 1-30 minutes, compared with 8 at 121-150 minutes, with the same sample size), its foraging strategy at this time is important, and in nature, it would forage solitarily on the small items of food I found it collecting in chapter five. It is thus valid to group *C. gigas* and *O. transversa* as solitary foragers, and assume that *D. intricatum* is primarily a solitary forager.

The other ants in the community may all be regarded as recruiters, although there are several *Polyrhachis, Camponotus* and one *Aphaenogaster* species which are likely to be solitary foragers, but their frequency of occurrence was not sufficient to test them. Abundances of all species on different baits are in appendix 4. Species with the highest modal abundance scores are primarily in the subfamily Dolichoderinae, except for some *Crematogaster* species, and *Pheidologeton,* the South East Asian marauder ants.

On the bait with most records of ant visits, glp, the highest proportion of the species have a modal abundance score of 1. On tlp, the most species have a score of 3. Solitary or near solitary foraging thus dominates the litter level fauna. The species of highest abundance are all primarily vegetation species, with the exceptions of *Pheidologeton* and *Lowriella.*

Table 4.6: Results of G-test of goodness of fit of predicted abundances of three species of ant at baits based on the Poisson distribution. d.f.=2

Species	time (mins)	G	p	observe more or less than expected randomly?
C. gigas	1-30	1.34	NS	
D. intricatum	1-30	0.83	NS	
O. transversa	1-30	24.05	<0.001	less
C. gigas	121-150	0.93	NS	
D. intricatum	121-150	9.64	<0.01	more
O. transversa	121-150	8.59	<0.025	less

Investigation 3: Foraging strategies: how do taxonomy and abundance relate to foraging success and behavioural dominance at baits?

ANALYSIS

Foraging success may be measured in several ways. These include persistence at food resources, choice of higher quality baits and access to or food removal from the bait. These parameters may be correlated with behavioural characteristics such as modal abundance score and speed to locate baits. These may in turn be affected by the taxonomic group of the organisms involved; close relatives are often similar. How is success affected by behavioural parameters of the species involved, and how do these relate to taxonomic grouping?

Behavioural parameters of species were measured as follows:

Percentage persistence for a species on a bait at a point =

$$\frac{\text{number of persistences}}{\text{number of opportunities to persist}} \times 100 \qquad \text{(eq. 4.1)}$$

where: opportunities to persist are occurrences on a bait at a point where a sample was taken later, and persistence is occurrence in successive samples.

Mean percentage persistence for a species on a given bait =

$$\frac{\sum \text{all \% persistences}}{\text{number of points where species had any opportunity to persist}} \qquad \text{(eq. 4.2)}$$

Where persistence of one or more species was related to the presence of other species, I measured the persistence from a given sampling time when the other species were/was present, to the next sampling time.

Time to appear for a species was the mean value of the time in minutes at which the species was first observed at baits.

a) How do behavioural parameters vary across subfamilies?

I performed factorial anovas to examine the difference in means of three behavioural parameters- abundance, persistence and time to locate baits, between subfamilies, on both glp and tlp. Residuals were normalised by transformation of data if necessary (transformations are noted in the results).

b) How are subfamily, mean percentage persistence of a species, time to locate baits and mean abundance at baits related?

For the baits glp and tlp, I performed simple regression analyses on mean abundance, mean percentage persistence, and time to appear at baits. Where there were significant differences in the abundance and persistence of subfamilies on glp, I first subtracted the subfamily mean, a technique known as phylogenetic subtraction (Stearns, 1983): this reduces the risk of spurious correlations among variables due to values being more similar among more closely related organisms (subfamilies), and differing between groups.

RESULTS

a) On glp, subfamilies differ significantly in their species' mean abundance and mean percentage persistence (tables 4.7, 4.8 and 4.9)

Table 4.7: Results of factorial anova on the mean abundances of species in four subfamilies

	glp: p<0.001		tlp p=0.0943	
subfamily	mean	SE	mean	SE
Formicinae	1.76	0.15	2.35	0.23
Ponerinae	1.80	0.38	-	-
Dolichoderinae	3.81	0.34	3.2	0.60
Myrmicinae	2.64	0.18	3.23	0.23

Table 4.8: Results of factorial anova on mean percentage persistence for glp, mean percentage persistence^2 for tlp, of species in four subfamilies

	glp: p=0.0039		tlp: p=0.41	
subfamily	mean	SE	mean	SE
Formicinae	22.56	6.58	3127.28	852.48
Ponerinae	22.66	8.69	-	-
Dolichoderinae	81.49	12.74	5780	2002.1
Myrmicinae	37.53	7.53	5110.11	965.23

Table 4.9: Results of factorial anova on square root of time to appear (minutes) of species in four subfamilies

	glp: p=0.28		tlp: p=0.31	
subfamily	mean	SE	mean	SE
Formicinae	10.07	0.74	9.82	0.51
Ponerinae	9.41	0.45	-	-
Dolichoderinae	9.17	1.07	11.4	1.01
Myrmicinae	8.24	0.56	9.48	0.70

These results are illustrated in figs 4.10 and 4.11:

Fig. 4.10: Mean abundance with standard errors for four subfamilies on glp

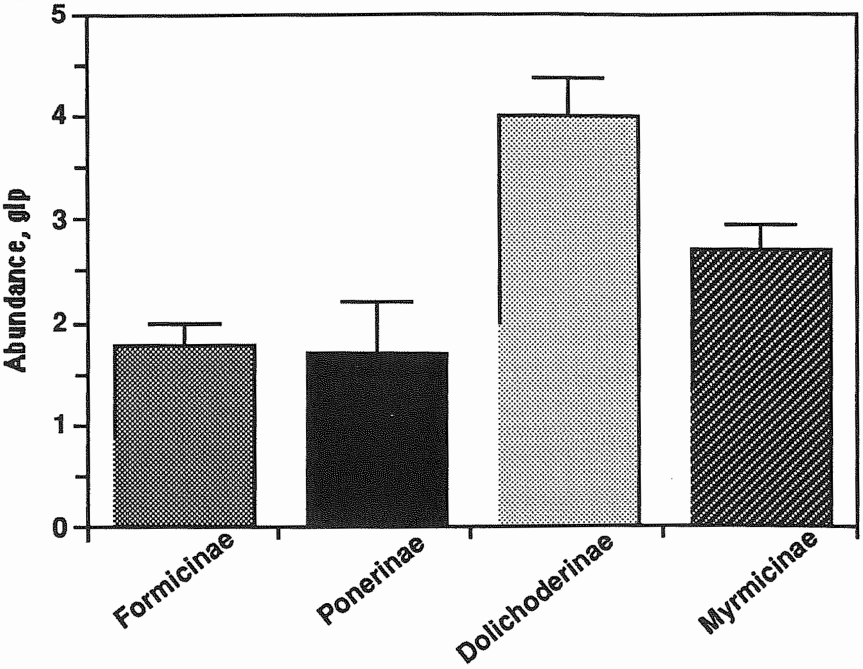
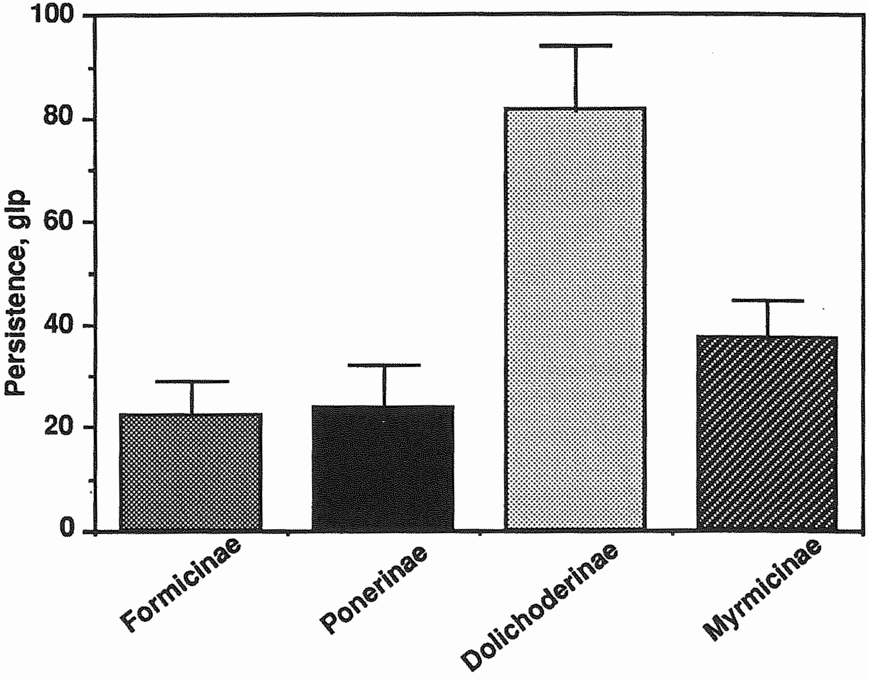


Fig. 4.11: Mean percentage persistence with standard errors for four subfamilies on glp



b) There is a highly significant positive relationship between mean abundance and mean percentage persistence on glp and and tlp, and a negative relationship between mean abundance and time taken to appear at baits on tlp: species of higher abundance arrive faster (table 4.10).

Table 4.10: Results of simple regressions of three behavioural parameters on glp and tlp. Superscripts indicate tranformations: 1 = variable after phylogenetic subtraction, 2 = square root of variable, and 3 = square of variable.

		glp				tlp	
interaction	coefficient	SE	p	interaction	coefficient	SE	p
^{1}abundance/ ^{1}persistence	0.017	0.002	<0.0001	abundance/ ^{3}persistence	1.67E-4	3.41E-5	<0.0001
^{1}abundance/ ^{2}time to appearance	-0.007	0.033	0.84	abundance/ ^{2}time to appearance	-0.168	0.058	0.0059
^{1}persistence/ ^{2}time to appearance	-0.431	1.38	0.76	^{3}persistence/ ^{2}time to appearance	-105.178	240.183	0.66

These relationships are illustrated in figs 4.12, 4.13 and 4.14 below.

Fig 4.12: Regression of mean abundance and mean percentage persistence on glp. Transformations as table 4.10

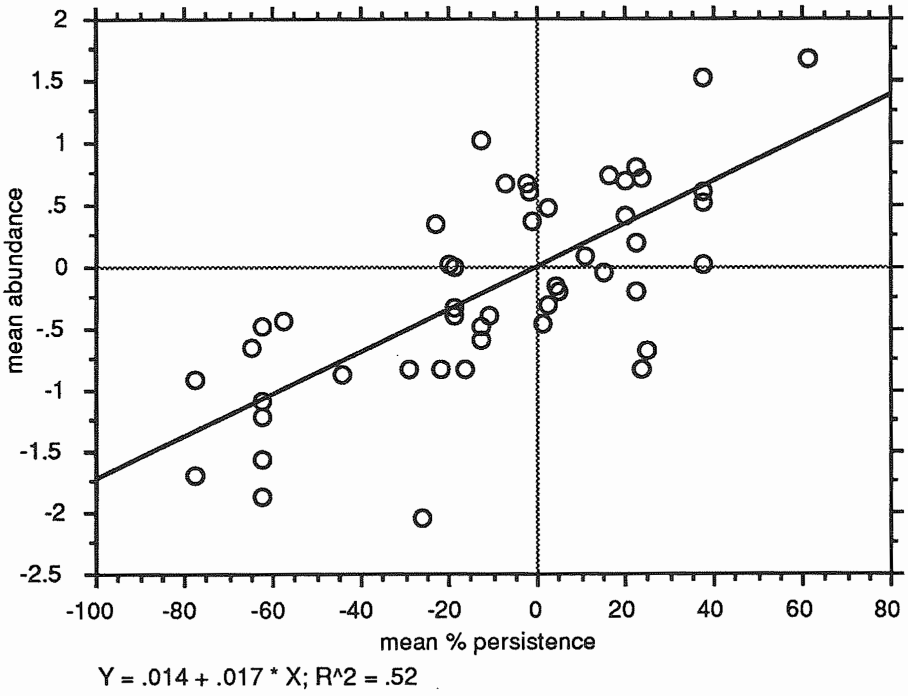


Fig 4.13: Regression of mean abundance and mean percentage persistence on tlp. Transformations as table 4.10

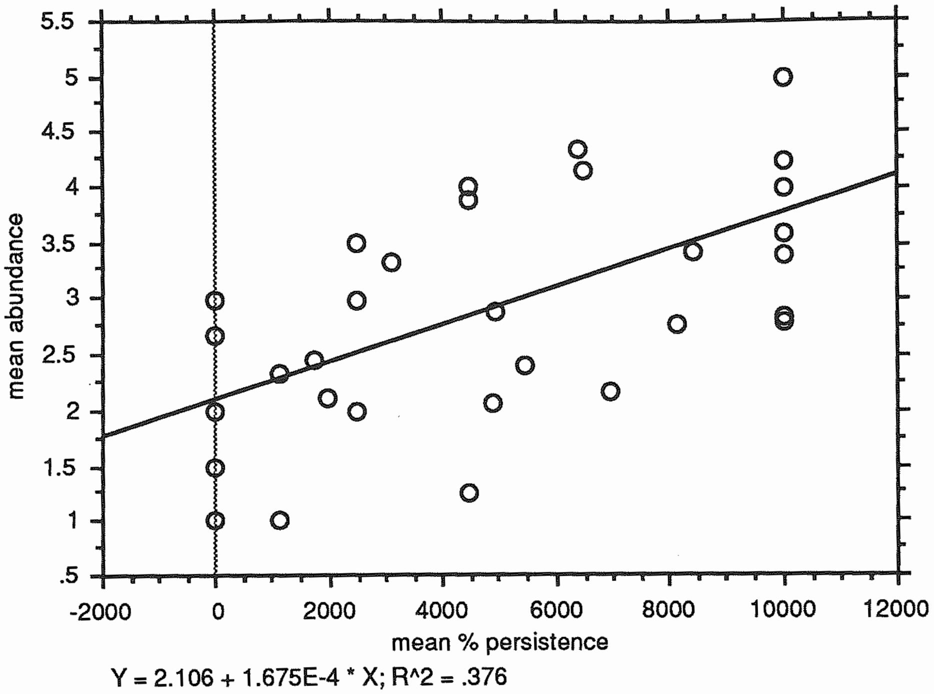
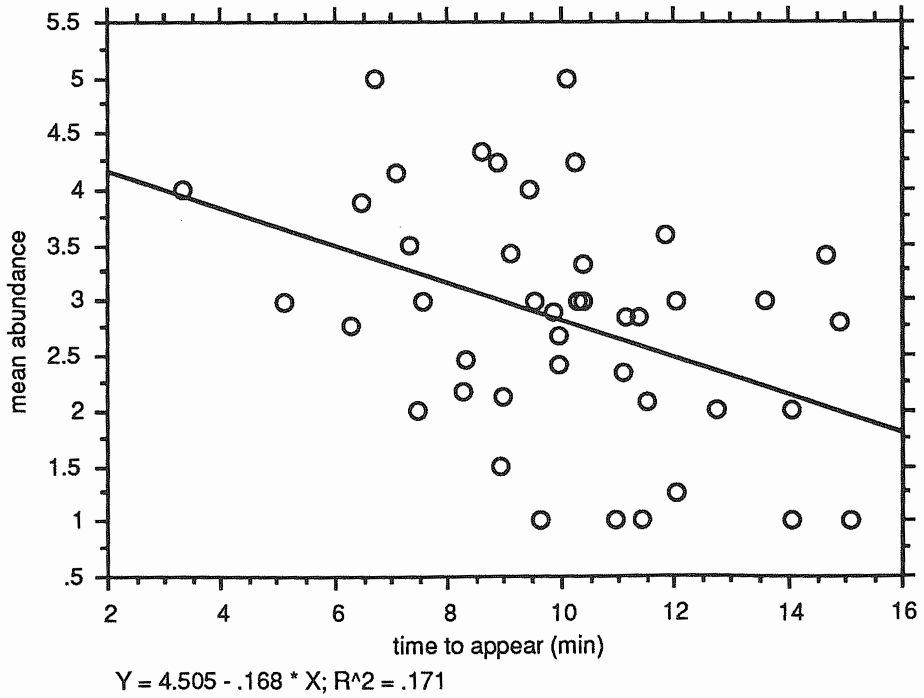


Fig 4.14: Regression of mean abundance and time to appear on tlp. Transformations as table 4.10



Investigation 4: Species interactions

ANALYSIS

a) Is there variation in the effect of other species on the persistence of a given species at a bait, and in the effect of a given species on others, and if so, how do subfamily and modal abundance explain it?

G-tests of contingency with Williams' correction were performed to test two aspects of each species inetrspecific interactions, on glp: How persistence of a given species depends on the presence of other species, and how persistence of other species depends on the presence of a given species. The data for modal abundance score classes (1-2 and 3-5) and subfamilies (Dolichoderinae, Myrmicinae, Formicinae and Ponerinae) were analysed.

i) A contingency table for each species was constructed a follows:

		other species	
		present	absent
species x	persists	a	b
	does not persist	c	d

ii) A contingency table for each species was constructed a follows:

		species x	
		present	absent
other species	persists	a	b
	does not persist	c	d

b) What are the relationships between mean abundance, mean percentage persistence, time to appear and the number of other species occurring with a given species at a point?

Regressions were used to examine the relationship between the mean abundance, mean percentage persistence and time to appear of all species on glp and tlp with number of other species occurring on the bait that day. Variables were transformed in the same way as in other parametric analyses (see table 4.10). "Other species" data was logged.

c) Are there negative associations of abundant species with each other and with less abundant species at points?

Association analyses were performed on occurrences of species or species groups with each other on glp. Species/groups and their cooccurrences were analysed by comparing them to random expectation using a chi-squared test with Yates correction according to Ludwig and Reynolds (1988). A table of values was arranged for each interaction thus:

		species/group B		
		present	absent	
species/group A	present	a	b	m = a + b
	absent	c	d	n= c + d
		r = a + c	s = b + d	N = a+b+c+d

and

$$\chi_1^2 = \frac{N\left[\left|(ad)-(bc)\right|-\left(N/2\right)\right]^2}{mnrs} \quad \text{(eq. 4.3)}$$

This association analysis was used to answer the following questions:

i) Are species of modal abundance 3-5 (good recruiters) negatively associated with each other on glp at points over a day, i.e. do potentially dominant species exclude each other from sampling points in the hectare? Species of high abundance score were split into four subfamilies and the co-ocurrences of each pair of subfamilies and some of the more frequently found genera and species were analysed. Data for all samples from each point over a day were combined as individual data values.

ii) Are species of high modal abundance positively or negatively associated with species of lower abundance (poorer recruiters)? All species of high modal abundance were grouped and the occurrence of all species, more frequent genera and individual species of lower modal abundance (1-2) with the species of high modal abundance was analysed.

d) How is foraging success of solitary foragers affected by the presence of all other species?

As solitary foragers are often not very persistent because they have to return to the nest frequently, their foraging success should be measured differently to the recruiting species. I measured success in the following way: when an individual of 3 selected solitary foraging species approached or was found on the bait, I timed its length of stay on the bait: longer than 5 seconds and/ or removal of food was deemed a successful attempt. Anything less was marked as a failure.

I used G-tests of contingency with Williams' correction to test whether the success of foraging attempts was affected by the presence of other species.

RESULTS

a) i) and ii) On glp, whether viewed by subfamilies or modal abundance score groups, there is a universal trend for all types of species persistence to be negatively associated with the presence of all other species, and for the presence of given species to be associated with the poorer persistence of others (tables 4.11 and 4.12). It is not possible to ascertain a causal link from this result however, and the direction of causation may differ between groups. There was no significant pattern on tlp, possibly due to small sample size.

b) No significant effect of any behavioural parameter on numbers of other species occurring on the bait was found on glp, but on tlp a significant positive effect of species' mean abundance was found: more other species occurred with species of higher abundance than expected (table 4.13).

Tables 4.11 and 4.12: The results of G-tests of contingency on pooled data of I) the dependence of persistence of a species on the presence/ absence of other species, and II) the dependence of persistence of other species on the presence of the given species, for glp and tlp (blank results indicate zero values in the contingency table)

glp, I		G	p	type of interaction
modal abundance score:	score 1-2 species	27.10	<0.005	negative
	score 3-5 species	5.17	<0.025	negative
subfamilies:	Dol	10.35	<0.005	negative
	For	4.91	<0.05	negative
	Myr	8.59	<0.005	negative
	Pon	14.56	<0.005	negative

glp, II		G	p	type of interaction
modal abundance score:	score 1-2 species	23.79	<0.005	negative
	score 3-5 species	18.04	<0.005	negative
subfamilies:	Dol	50.36	<0.005	negative
	For	3.98	<0.05	negative
	Myr	27.72	<0.005	negative
	Pon	9.91	<0.005	negative

tlp, I		G	p	type of interaction
modal abundance score:	score 1-2 species	3.78	NS	none
	score 3-5 species	0.54	NS	none
subfamilies:	Dol	-	-	-
	For	1.58	NS	none
	Myr	0.35	NS	none
	Pon	-	-	-

tlp, II		G	p	type of interaction
modal abundance score:	score 1-2 species	0.26	NS	none
	score 3-5 species	1.05	NS	none
subfamilies:	Dol	0.06	NS	none
	For	1.24	NS	none
	Myr	0.17	NS	none
	Pon	-	-	-

Table 4.13: Regression of numbers of other species on three behavioural parameters for tlp. Superscripts indicate transformations: 1 = log of variable, 2 = square root of variable, and 3 = square of variable.

	tlp		
interaction	coefficient	SE	p
^{1}other sp./ abundance	0.18	0.069	0.023
^{1}other sp./ ^{3}persistence	0.47E-5	2.23E-5	0.054
^{1}other sp./ ^{2}time to appearance	0.001	0.037	0.97

c) i) No significant negative or positive associations were found between groups of species, genera or individual species of high abundance (potentially dominant species), i.e. these species do not occur together in numbers other than would be expected randomly.

and ii) No significant negative or positive associations of any species or species groups of high abundance and low abundance were found on glp at points over a day, i.e. potentially dominant species are not found significantly more or less than expected by chance with poorer recruiters.

d) Table 4.14 shows that in two of the three solitary foraging species, presence of other species is significantly associated with decreased foraging success.

Table 4.14: Results of G-tests of contingency with Williams' correction on the foraging success of three solitary species on glp

species	G	p	pattern
Camponotus gigas	9.82	<0.005	less successful in presence of others
Diacamma intricatum	1.13	NS	none
Odontoponera transversa	50.7	<0.005	less successful in presence of others

Investigation 5: How do species composition and foraging success vary with time?

ANALYSIS

a) Do species of different modal abundance scores/subfamilies occur at times different to random expectation?

I performed G-tests of contingency with Williams' correction on the points attended by species in abundance scores 1-2 and 3-5, and the 4 subfamilies up to 60 minutes and after 60 minutes, on glp.

b) Does the persistence of species with different modal abundance scores/ in different subfamilies change differently to random expectation early (0-60 minutes) and late (60 minutes onward)?

I tested the difference in proportion of persistences/ the number of opportunities to persist on glp, using the method in Zar (1984) (see above), for each species and on pooled data for modal abundance score groups and subfamilies, for the two time intervals.

c) Are there patterns of change in diversity and species rank/ abundance over time?

Species rank/ log abundance plots for three time intervals, 1-30 minutes, 91-120 minutes and 181-211 minutes were inspected to find any obvious patterns in dominance/ evenness over time. Four diversity indices: the Shannon-Wiener, the Berger-Parker and Simpson indices and the Q-statistic were calculated for successive time intervals. These indices were chosen for their variation in properties, namely discriminant ability, what they measure (dominance or diversity) and sensitivity to sample size (Magurran, 1988). The relationships of the indices with sample size and time were examined using multiple regressions. This was done to establish the sensitivity to sample size and the detection of changes in the community over time.

RESULTS

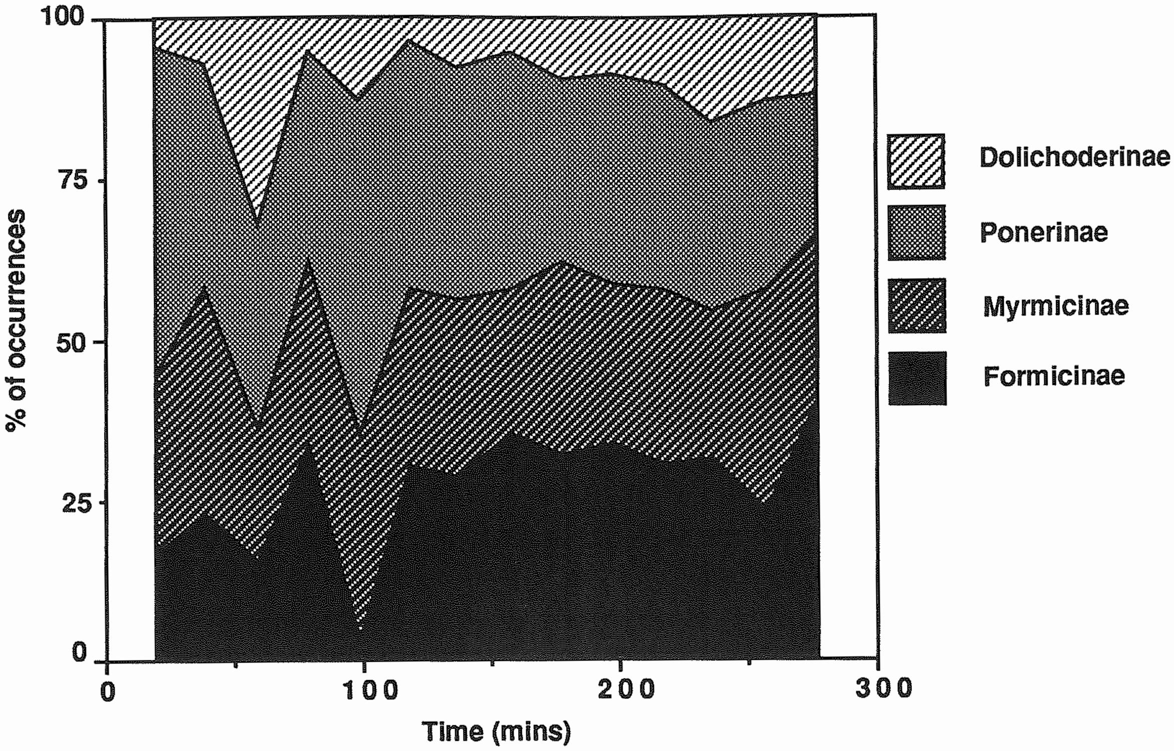
a) Formicinae occur significantly more in later samples, and Ponerinae occur more earlier (Table 4.15)

Table 4.15: Results of 2 G-tests of contingency with Williams' correction on the occurrence of species early and late in the sampling time on glp

split by	G	p	pattern
modal abundance scores	0.141	NS	none
subfamily	47.05	<0.005	Formicinae occur less earlier, Ponerinae occur more earlier

The relative proportions of subfamilies over time an be seen in Fig 4.15.

Fig 4.15: Relative proportions of subfamily occurrence over time.



b) Table 4.16 shows the results of testing the proportions of persistences/ opportunities to persist for *Odontoponera transversa* (the only significant result for a species) and for subfamilies and modal abundance score groups.

Table 4.16: The results of testing the proportions of persistences/ opportunities to persist for *Odontoponera transversa*, and for subfamilies and modal abundance score groups.

species/ group	Z	p	difference and standard error	pattern
Odontoponera transversa	2.45	<0.02	0.19±0.12	persistence greater earlier
Dolichoderinae	-3.19	<0.002	0.35±0.22	persistence greater later
Formicinae	-1.41	NS		
Myrmicinae	-1.53	NS		
Ponerinae	1.50	NS		
modal abundance 1	2.42	<0.02	0.11±0.09	persistence greater earlier
modal abundance 2	0.79	NS		
modal abundance 3	-3.11	<0.002	0.30±0.19	persistence greater later
modal abundance 4	-0.31	NS		
modal abundance 5	-2.36	<0.02	0.14±0.12	persistence greater later

c) In order to investigate whether community patterns in diversity and species/rank abundance change over time during succession at the baits, species rank/abundance plots were drawn and diversity measured at each time interval. The plots for three time intervals can be seen in Figs 4.16 - 4.18. There are slight changes in species/ rank abundance plots over time.

Fig 4.16 : species rank/ log abundance plot for time interval 1-30 minutes

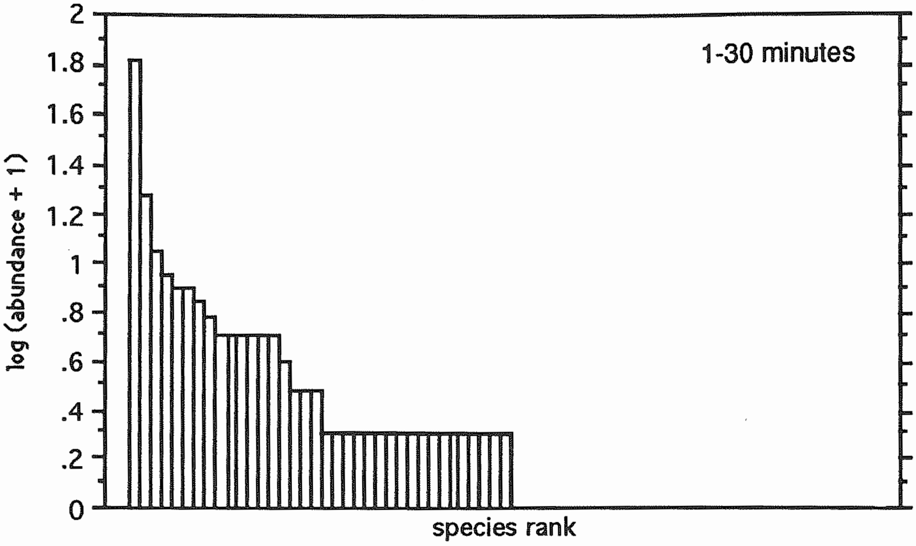


Fig 4.17 : species rank/ log abundance plot for time interval 91-120 minutes

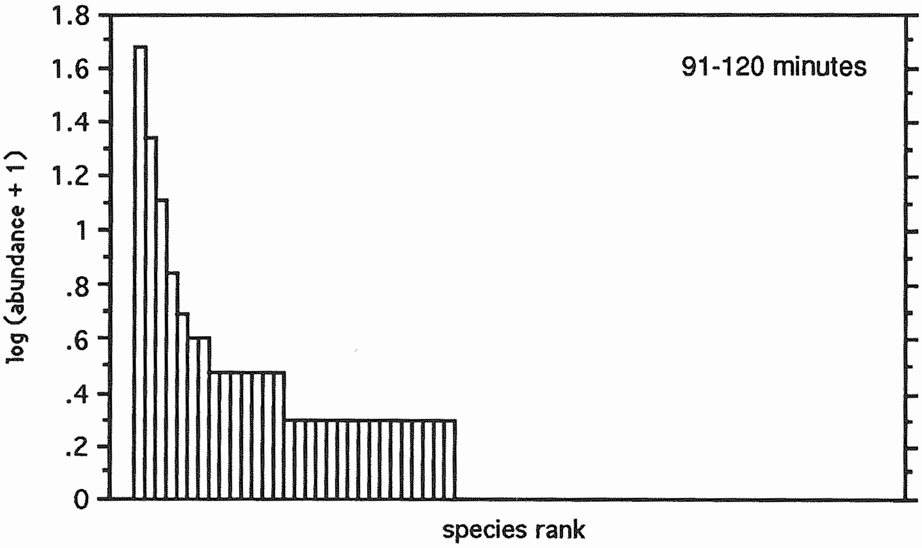
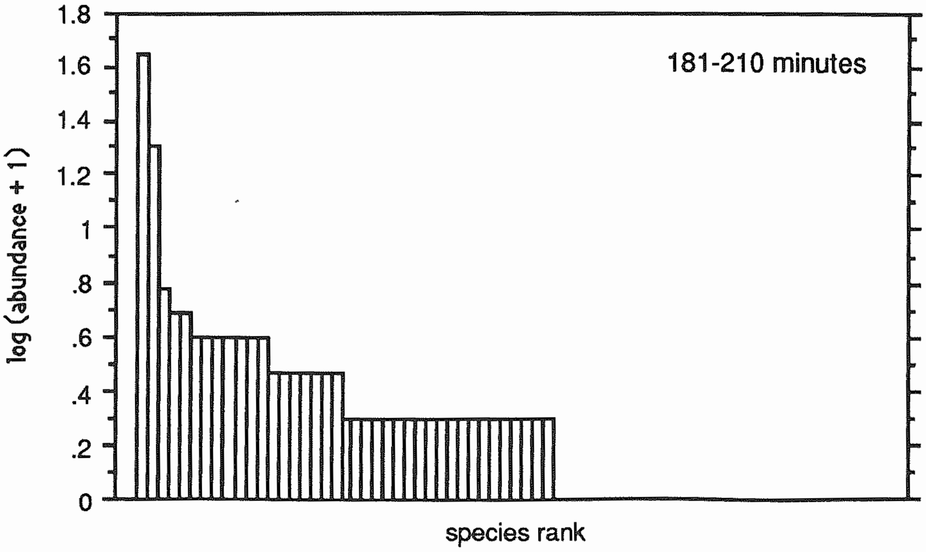


Fig 4.18 : species rank/ log abundance plot for time interval 181-210 minutes



There was some evidence that species rank abundance changes over time: seven species exceed log abundance 0.8 at 1-30 minutes, four species at 91-120 minutes and two at 181-210 minutes.

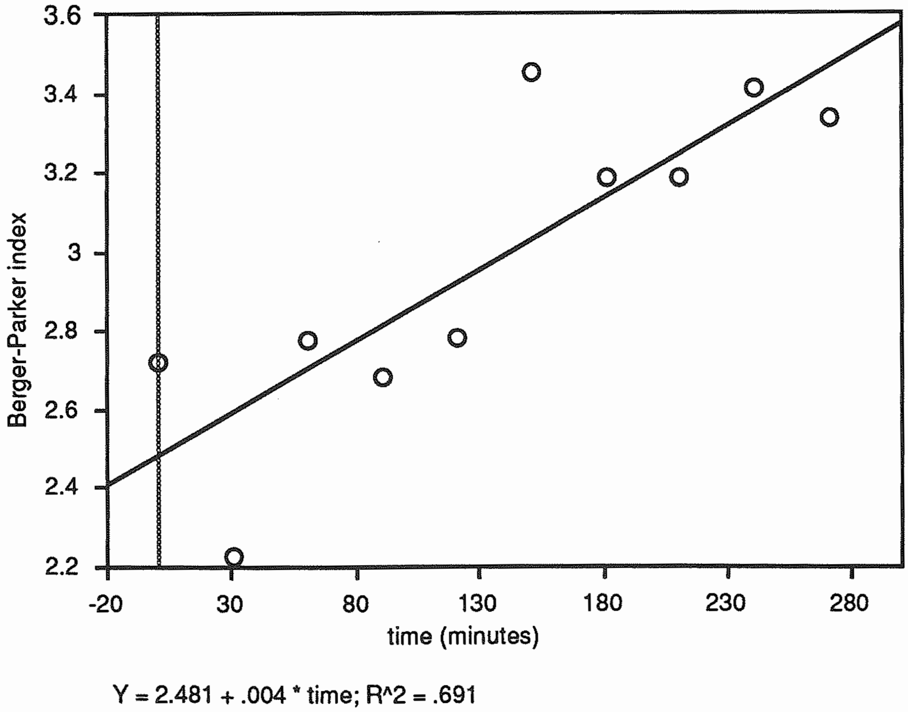
The changes in diversity over time were investigated using four diversity indices. In order to see whether sample size has a strong effect on the indices, multiple regression was used. Table 4.17 shows the results of a multiple regressions of the sample number and time on the diversity indices.

Table 4.17: p-values from multiple regression for effects of sample number and time for four diversity indices

	sample number:p-value	time:p-value
Shannon-Wiener (H')	0.0044	0.30
Simpson (1/D)	0.75	0.06
Berger-Parker (1/d)	0.13	0.002
Q-statistic	0.15	0.6

These results indicate that the Shannon-Wiener index is the most sensitive to sample size, and thus the least useful in comparing the different time intervals for my data, which differed in sample size. The Berger-Parker diversity index is the only index to show a significant pattern with time (see fig 4.19), presumably at least partly because it was not sensitive to sample size.

Fig 4.19: bivariate regression plot showing values of the Berger-Parker diversity index 1/d with time.



The significant change in this index over time can be attributed largely to the lessening occurrence of *Odontoponera transversa,* a solitary foraging ponerine, whose subfamily I showed to occur significantly more often earlier in the sampling time (see above), and the most frequent visitor to baits. The index is an inverse numerical dominance index, and directly shows the decrease in numerical dominance of this species. There is thus little overall change in diversity pattern with three indices, but the numerical dominance of *Odontoponera transversa* causes the Berger-Parker index to change with time.

Discussion

Patterns at baits

The higher abundance of ants on certain baits implies that the categories of bait quality which I chose to regard as higher (large, protein) and lower (small, carbohydrate) were indeed valid. Higher modal abundance was found to occur on trees and on large protein baits. There were more ant visits to ground baits, and large protein baits, compared with tree baits and small protein or carbohydrate baits. Bait quality was not found to cause any qualitative difference in the identity of species responding, at the subfamily level. Thus I found no patterns of the type found by Lynch (1980), Fellers (1987) or Savolainen (1988), where behaviourally dominant species were found more often on higher quality baits.

Fewer ant visits happened on the trees, giving fewer opportunities to test hypotheses due to small sample size.

Recruitment and foraging strategies

I found that three species, *Camponotus gigas* (sp. 1), *Diacamma intricatum* (sp. 2) and *Odontoponera transversa* (sp. 3), with a modal abundance score of 1, were solitary foragers. Other species likely to be solitary foragers include most *Polyrhachis* except spp. 39 and 40, many *Camponotus* species and *Aphaenogaster*. Appendix four shows that solitary foraging may be the the most frequent strategy on the ground, whereas recruiting to modal abundance 3 is the commonest pattern on vegetation. I have assumed that abundance at baits is an indication of recruitment ability. It is also lindicative of colony size, however. The lower overall abundances seen on the ground may be due to smaller nest site cavities of litter dwelling species (see chapter two), and their smaller colonies, compared with large colonies of, for example, *Crematogaster*, (personal observations) which live in large plant cavities. However, many apparently solitary foragers, such as the *Polyrhachis* and *Camponotus* species, are large bodied. This may mean that solitary foraging is an ecological adaptation to foraging in the very speciose litter layer.

All of the studies discussed above showed that species of lower abundance are less aggressive and dominant, and this may be an advantage when encountering so many other species during foraging. Studies of strongly hierarchically structured arboreal ant communities (reviewed by Majer, 1993) invariably find that dominants have large colonies and recruit well. This fits with my finding of higher abundances on trees.

The highest abundances occurred in the subfamily Dolichoderinae and Myrmicinae: *Dolichoderus, Lowriella* and *Philidris* were all highly abundant where they occurred yet infrequent, as was *Pheidologeton,* whereas *Crematogaster* occurred with reasonable frequency, and was largely responsible for the greater average abundance on trees[1]. It is interesting to note that most studies on the behaviour of species occurring in the Oriental area largely concentrate on the highly abundant but infrequent species (in primary forests): Moffett (1988) studied *Pheidologeton*, Sabina Steghaus-Kovac is currently completing work on *Leptogenys,* Hölldobler (1983) studied *Oecophylla,* and Maschwitz and Hänel (1985) studied *Dolichoderus*.

Behavioural correlations

Significant taxonomic differences in mean abundance and mean percentage persistence were found for ants on glp, but on the trees, there was no significant difference. There was a significant positive relationship between abundance and persistence on glp and tlp, and a negative relationship between abundance and time taken to locate the bait on tlp: more abundant species arrive faster. This agrees with the findings of Savolainen and Vepsäläinen (1988) for dominant species, but disagrees with Fellers (1987) where dominant species arrive later.

Species interactions

All species, whether arranged by subfamily or modal abundance score, persist less with other species present, and other species persist less with them present. There is no difference in the effect of species of higher and lower abundance on other species persistence, as expected from all the studies listed above, or of all species on the persistence of species of low or high abundance.

On tlp, increased mean abundance is correlated with increased numbers of co-occurring species (surprisingly). This may be a microhabitat preference effect: larger trees can support both larger colonies and more colonies. I sampled many small trees, and some larger ones. Thus it appears that the species are positively associated. Analysis controlling for tree size may remedy this problem. Harada and Adis (in prep) have proposed that tree trunks are extremely important in movement of ants around the forest. It is also possible that some ant species are attracted to food by other ant species, using them as scouts (Reznikova, 1982), although this is less likely. There was no evidence for groups or species of high modal abundance being non-randomly associated, or differing in their associations with other high abundance species and low abundance species. This disagrees particularly with Bose and Davidar (1990), in which negative associations of dominant species but not submissive species was the primary significant pattern.

Two of the three solitary foraging species, *Camponotus gigas* and *Odontoponera transversa*, were found to forage less successfully in the presence of than in the absence of other species.

Time

Formicinae were found to occur less earlier, and Ponerinae more so. This may imply submissiveness of the Ponerinae in this study: *Odontoponera transversa* also persisted more earlier, and Dolichoderinae less so. *D. intricatum*

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[1] Some species of *Crematogaster* and *Camponotus* were positively associated with each other: the species nest in the same tree holes and forage together. This has been found in other communities (Hölldobler and Wilson, 1990).

occurs much more in the first half hour of sampling than at any other time (around 50% of its occurrences), but *C. gigas* occurs equally over all time slots. The Ponerinae may be arriving at the baits earlier and opportunistically exploiting them before the Dolichoderinae, of higher abundance, or the recruiting Formicinae, arrive and take over. Species of modal abundance score 1 persisted more earlier, and those of scores 3 and 5 persisted less earlier. This further strengthens the evidence for an opportunistic role for the commoner Ponerinae in this habitat. These temporal patterns would not be expected from the diel cycles of *Odontoponera transversa* and *Diacamma intricatum* (chapter five).

Species rank-abundance plots showed a slight decrease in evenness over time. The Berger-Parker diversity index was found to be relatively insensitive to sample size and is a good index with which to assess diversity (actually inverse numerical dominance) changes over time. The positive relationship of the index with time, was due to a decrease in the dominance of samples by *Odontoponera transversa* . This is in contrast to the pattern shown by species rank-abundance plots.

The results of these investigations into the presence of a hierarchical arrangement of interspecific interaction all proved negative: there was no evidence that more abundant species have a stronger effect on the persistence of other species; that numbers of co-occurring species are reduced more in the presence of more abundant species, or that more abundant species are more negatively associated with other more abundant species than with less abundant species.

Most studies of tropical behavioural interactions in ant communities are performed in secondary forests or plantations (Leston, 1973a; Room, 1975; Jackson, 1984; Majer, 1993). According to the dominance impoverishment rule, (Wilson, 1990), these habitats and the temperate ones above, with fewer species, are more subject to strong behavioural interactions governing community structure, and often include very aggressive species such as *Oecophylla* sp.: these species are usually not found in undisturbed primary forests at ground level. My only sample of *Oecophylla smaragdina* came from degraded secondary forest away from my study site: I observed far more aggression here than in the primary forest (personal observations). However, these rules do not seem to apply in the Australian seasonal tropics (Andersen, 1992) where high species diversity is accompanied by high levels of dominance, largely by *Iridomyrmex* spp. and *Oecophylla smaragdina,* but primarily on the savannah, and much less in the forest.

It therefore appears that the evidence for a structured competitive hierarchy in this community is weak, although some lesser behavioural and temporal traits may be evidence of predictable patterns of food resource use and temporal occurrence. The factors governing this tropical community at baits are not immediately apparent as a hierarchical and interactive set of species. Levels of aggression were very low.

Wilson (1990) reviews the factors that have made social insects so successful compared to other taxa: series parallel operations, worker sacrifice, superior resource inheritance and social homeostasis and flexibility have enabled social insects to compete successfully for resources in communities and come to numerically dominate many of them. The most speciose genera in the world, *Camponotus*, *Pheidole* and *Crematogaster* are all known to be very variable in life style and adaptations (Wilson, 1976), with no obvious physical or behavioural adaptations to enable them to achieve the rank of most prevalent genera: he proposes that the success of these genera comes from ecological diversification and/ or ability to out compete other genera biogeographically. In this habitat, the Myrmicinae, including both *Pheidole* and *Crematogaster*, figured notably little at the extremes of any of the parameters investigated in this study: their great diversification of behaviours and lifestyles means that their overall behavioural characteristics were ill defined in one direction or another, and they may be broadly equated with the 'generalised Myrmicinae' of Greenslade (1978).

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CHAPTER FIVE

Interspecific colony dispersion and niche relations of three large tropical rain forest ant species

Introduction

Since the pioneering work of Lotka (1932) and Volterra (1926) on predictive models of coexistence of competing organisms, and competitive exclusion experiments by Gause (1934), competition and resource partitioning have frequently been regarded as major forces structuring communities. These concepts have been investigated in three major ways: workers have searched for 'substantial differences' in the niches of supposedly competing species (Schoener, 1986); empirical data on niche distributions have been compared with null models in which niches are distributed at random (May, 1984); and theoretical studies have been used to predict exactly how much overlap is permissible for species to coexist (MacArthur and Levins, 1967).

Most workers have adhered to Hutchinson's (1957) definition of the niche as a 'multi-dimensional hypervolume' of space within the limits of tolerance of factors that affect an organism's survival; Pianka (1981) summarises the definitions. Today, the niche is commonly defined as a 'utilisation distribution' (Giller, 1984; Schoener, 1986; Arthur, 1987), or frequency histogram, of food size classes, for example.

The relationship between niche overlap and competition between species has been quite confused in the past (Schoener, 1974), some authors recently concluding that the magnitude of overlap as an indicator of the level of competition (Schoener, 1986; Keddy, 1989) should be regarded with caution.

The sorts of resources which have been found to be significantly partitioned in communities include habitat or micro-habitat, food type or size, and time, in that order of importance (Schoener, 1986; Pianka, 1969). This is because altering spatial utilisation has the lowest cost/ benefit ratio of all resource types. Not feeding at any time costs most of all. Schoener (1986) notes that the organisms most likely to be partitioned by time include predators and ectotherms. This partitioning is less likely as species number increases. Those with a relatively high prey size/ body size ratio are often partitioned by prey type.

Workers usually choose to investigate niche relations in species of the same 'guild' (Root, 1967). These are groups of species, the members of which are similar in their trophic roles, and which interact weakly with other guilds (Pianka, 1983).

However, despite the interest in resource partitioning as a mechanism enabling coexistence in communities, Arthur (1987) reminds us that there are at least five methods of attaining stable coexistence in communities, resource partitioning is only one of them.

Lynch et al. (1980) examined ecological segregation in a guild of surface foraging, generalist ants in north American temperate forests: they found that the less aggressive species overlapped less in their resources with the most aggressive species, and that the weakest competitors had broader niches, an assumption of the competitive hierarchy model of community structure (Keddy, 1989). However, Culver (1974) found no relationship between niche width and aggressiveness. Differential use of food sizes and type has been found to be an effect of differential desiccation resistance, body size, nest site and activity, and to promote coexistence in a grassland ant community (Hansen, 1978). Briese (1982) found that food type and time overlaps fluctuated greatly in response to environmental changes in semi-arid Australia, and that there was little evidence for exploitative competition. Marsh (1985) found the same patterns in Namibia. Davidson (1977) found that differences in foraging strategy allowed coexistence of ant species in north American deserts.

In this study, I examine the niche relations and interspecific dispersion of a guild of three large, generalist, solitary foraging, ground nesting ants, *Camponotus gigas* (subfamily Formicinae), *Diacamma intricatum* and *Odontoponera transversa* (both Ponerinae) in a hectare plot in Bruneian primary dipterocarp rain forest. These species were common at all primary lowland dipterocarp rainforest sites, at all times of year, at baits, in pitfall traps and in litter samples. The following questions were tackled:

1) Is there any evidence of negative interspecific interactions spatially or at baits?

2) Does this guild of species' niches overlap substantially?

3) Could resource overlap and interspecific interactions be related?

We might expect that low niche overlap would promote coexistence between the species, and that any negative interactions between them might be evidenced by relative nest distributions and associations at baits: if avoiding each other, nearest neighbour nests of different species would be situated further away from each other than expected randomly, and the species would forage less together.

This study was also intended to be descriptive, as we have very little idea of what tropical rain forest ant species do, and especially what they eat (Naomi Pierce, pers. comm.).

The resources used in the analysis were food (type and size), space (vertical foraging range) and time (diel cycle) (Schoener, 1974).

Methods

FIELDWORK

The fieldwork took place in June-December 1992. Nest entrance distributions of the three species of ant were mapped by following sardine baited foragers to nest entrances in the hectare, and noting locations of colony entrances on a map of the plot. If multiple nest entrances were found (only in the case of *C. gigas*), the geometric centre of these was noted as the colony location. The whole 100x100m was mapped for *C. gigas* (45 colonies), a 60x60m area for *D. intricatum* (62 colonies) and a 40x40m area for *O. transversa* (367 colonies). It was not feasible to map the whole hectare for all species, particularly *O. transversa*. As the frequencies of all three species were found to be even over the hectare at baits, I considered it valid to implement the randomisation procedure described below on a section of the whole hectare's ant colonies. Interspecific nearest neighbour nest distances of 45 pairs of *Camponotus-Diacamma, Camponotus-Odontoponera* and *Diacamma-Odontoponera* were recorded.

Food samples were collected as follows: food items carried by returning foragers were collected at the nest entrance of the three species (at least 6 colonies of each species were sampled), during the day and after dark, and preserved for later examination in 80% alcohol. Samples were measured and identified in the lab.

Use of space was assessed by placing protein and carbohydrate baits at 100 points at two levels in the hectare plot, on the litter and at eye level on tree trunks, and recording occurrences of these species at the baits, day and night. This was repeated three times. I visited each bait only once in the day or in the night, in order to keep each observation independent.

Diel cycles were recorded by observing ant activity at the nest entrance throughout four 24hr cycles. All entrances and exits were recorded for four different colonies of each species.

ANALYSES

Interspecific Nest Entrance Dispersions

It was not possible to assess the interspecific association of the three species in the same way as chapter three i.e. by using a G-test of contingency, because numbers of colonies per unit area were so vastly different for each species, and mapping an entire hectare of *O. transversa*, around 3000 nest entrances, was not feasible. I therefore decided to approach the problem in a different way.

The median values of observed interspecific nest entrance distances of 45 nest pairs for each species combination were compared with 1000 randomised replicates of interspecific nest distances. For each replicate, the larger (bottom) map (*C. gigas* or *D. intricatum*) was replicated ninefold, and the smaller (top) map (*D. intricatum* or *O. transversa*) was effectively moved around relative to it, always keeping at least a small fraction of the smaller map inside the centre of the nine larger map replicates. Nearest neighbour nest distances for the pair of species were then calculated. The ninefold replication was used as the overlaid map was liable to go over the edge of the larger map when moved, and drastically alter inter-nest distances. It ensured that edge effects of the larger map were not a problem (Ryti and Case, 1992), as the distance from the edge of the smaller to the edge of the larger map replicates was always at least 20m. Edge effects caused by proximity of the larger map species to the edge of the smaller map were resolved by taking distances of nests only where the colony of the larger species fell inside the prescribed boundary of a central area (Fig. 5.1). Edge effects of this sort are otherwise liable to create spuriously high values for inter-nest distances (see chapter 3). The width of this boundary was 2m for *O. transversa* and 7.5m for *D. intricatum*. Colonies of the larger map species within the internal boundary of the smaller map species were selected and interspecific nearest neighbour distances calculated. This method also kept the colony distributions intact during replication. This was necessary as nest distributions could not be assumed to be random. This was repeated for each replicate (see fig. 5.2).

Fig. 5.1: Close up view of nearest neighbour relations in randomised replicates of two species nest distributions. The species of smaller area (b on fig. 5.2, open circles) is overlaid on the 9 larger species replicates (a on fig. 5.2, closed circles), e.g. *D. intricatum* overlaid onto *C. gigas*, or *O. transversa* on to *D. intricatum*. Valid internest distances are shown by lines joining the nests concerned. Invalid distances are shown by scored lines. Measurements are invalid if the larger species occurs outside the internal boundary area set for *D. intricatum* and *O. transversa.*

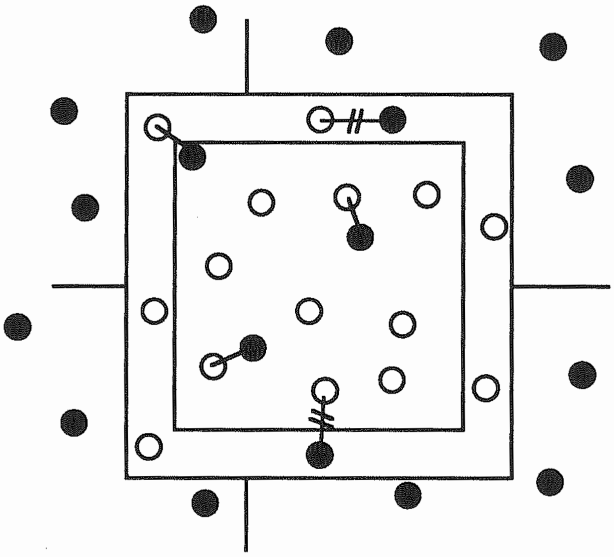
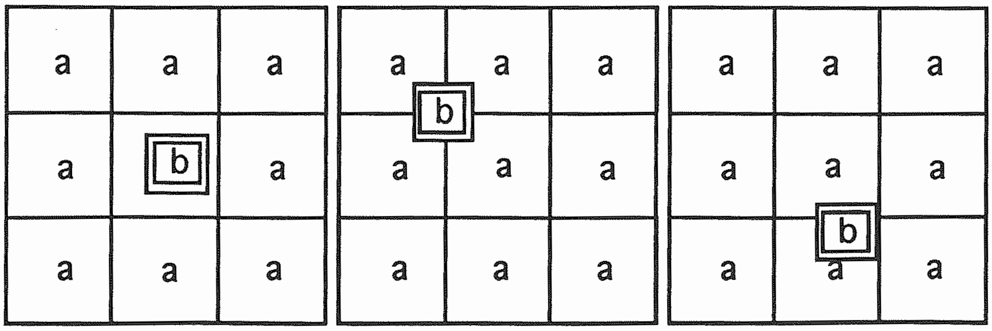


Fig. 5.2: Successive replications of randomised nearest neighbour distance calculations for two ant species' (a and b). Nearest neighbour distances between colonies of species a (larger ninefold replicated map) and b (smaller map) are calculated for colonies of species a occurring within the internal boundaries of the map of b.



The frequency distributions of 1000 randomised replicate medians were used to find directly the probability of the observed median result happening by chance. The number of randomised medians smaller or larger than the observed value were counted, and a p-value was calculated directly from this number. A negative association of nests (overdispersion) is shown when most randomised replicates are smaller than the observed value, and a positive association (clumping) when most randomised values are larger. The 0.05% level of significance (≤50 or ≥950 replicates) was used.

Species Association at Baits

In order to assess interspecific association between the three species of interest at baits, χ_1^2 contingency tests of association (Ludwig and Reynolds, 1988) were performed on presence/ absence data for the three two species interactions.

For each two species interaction, the following contingency table was constructed:

		species 1		
		present	absent	
species 2	present	a	b	a + b
	absent	c	d	c + d
		a + c	b + d	a + b + c + d

where: expected values (e.g. $E_{(a)}$ for cell a)

$$E_{(a)} = \frac{(a+b)(a+c)}{a+b+c+d} \qquad \text{(eq. 5.1)}$$

No correction for small sample size was necessary (Ludwig and Reynolds, 1988), because numbers were large.

Niche Breadths and Overlaps

It was assumed that resources were limited in availability. Niche width and resource overlaps for food size, food type, use of vertical foraging space and use of diel time were calculated. The Levins index of niche breadth was used (Krebs, 1989):

$$B_i = \frac{1}{\sum_{a=1}^{n} p_{ai}^2} \qquad \text{(eq. 5.2)}$$

where B_i= Levins niche breadth of species i; p_{ai} = proportion of use of resource class a by species i and n = number of resource classes.

As the index is maximal when all resource classes are used in equal proportion, the maximum possible niche breadths for each resource for each species were calculated. From this, an overall mean percentage niche breadth for each species was found.

The percentage overlap was calculated for each two species interaction (Krebs 1989):

$$p_{ij} = \left[\sum_{a=1}^{n} \left(\text{minimum } p_{ai}, p_{aj} \right) \right] 100 \qquad \text{(eq. 5.3)}$$

where p_{ij} = percentage overlap of species i and j; p_{ai} = proportion of use of resource class a by species i and n = number of resource classes.

Food size niche parameters were calculated from the probability distribution function generated from the mean and standard deviation of the logged food size data, in order to facilitate smoothing of the distribution. Food type overlap was calculated from the numbers of prey in each of the classes for each species. Time overlap was calculated for entrances and exits, and reduced to two classes of activity in the day and night (6am-6pm and vice versa). Space utilisation (foraging height) was calculated from the relative numbers of occurrences of each species at tree and ground baits, day and night.

Overall percentage overlap for each pair of species was calculated in the following way: as spatial utilisation data were dependent on day and night (time), overall percentage overlap in time and space was calculated as a single parameter for each species. The percentage overlap of each of four classes, ground bait/ day, ground bait/ night, tree bait/ day and tree bait/ night were calculated and added together to give this parameter (May, 1975). This percentage was then multiplied by those for food type and food size overlap to give an overall multiplicative percentage overlap. No inter-dependence of other resource axes were found for any of the species.

Results

Interspecific Nest Entrance Dispersions

Table 5.1 shows the results of 1000 replicated randomised tests on the medians of the interspecific nest entrance distances, and the kinds of interactions going on. There are no significant negative interactions, but the nests of the *D. intricatum* and *O. transversa* are significantly positively associated.

Table 5.1: Observed median inter-nest distances for three species pairs, numbers of randomised inter-nest median distances smaller than the observed median from 1000 replicates, probability and type of interaction happening between measured nests.

species pair	observed median (m)	number of randomised replicates smaller	p	association of observed nests
C. gigas/ D. intricatum	4.10	857	0.143	negative
C. gigas/ O. transversa	1.00	350	0.350	none
D. intricatum/ O. transversa	0.65	4	0.004	positive

Species Associations at Baits

Table 5.2 shows the probabilities of observed occurrences of species with each other, and whether interactions were positive or negative.

Table 5.2: Results of χ_1^2 test of interspecific association of three species with each other.

species	χ_1^2	p	interaction
C. gigas/ D. intricatum	0.29	NS	none
C. gigas/ O. transversa	22.10	<0.001	+
D. intricatum/ O. transversa	0.67	NS	none

C. gigas and *O. transversa* are significantly positively associated at baits.

Niche Breadths and Overlaps

Table 5.3 shows the food items collectes by the three species. Their food preferences, which differed, are illustrated in fig. 5.3. Over half *C. gigas*' diet consists of non animal matter, and the other species forage largely on insects which they predate.

Table 5.3: Percentage food items collected by three ant species. Numbers of samples were 101 for *O. transversa*, 105 for *D. intricatum*, and 101 for *C. gigas*.

Food items	*Odontoponera transversa*	*Diacamma intricatum*	*Camponotus gigas*
		% of diet	
Termites	18.80	29.80	4.95
Ants	26.70	11.54	6.93
Fungus	8.90	9.61	36.63
Faeces	0.99	0.96	12.81
Plant matter	5.90	6.73	8.91
Bees	6.93	6.73	3.96
Orthoptera	6.93	3.85	0
Bugs	0.99	1.92	1.98
Woodlice	3.96	0	0
Beetles	3.96	1.92	0
Spiders	2.97	5.70	3.96
Lepidoptera larvae	0.99	0	0
Lepidoptera	0	0	0
Ant pupae	1.98	0	0
Ant larvae	0	0	0
Earwigs	0.99	0	0.99
Other larvae	0.99	0.96	0.99
Centipedes	0.99	0	0
Other Hymenoptera	0	0.96	2.97
Neuroptera	0	1.92	0
Diptera	0	2.88	1.92
Insect remains	6.90	14.42	11.88

Fig. 5.3: Percentage food type utilisation of three common food types by the three species.

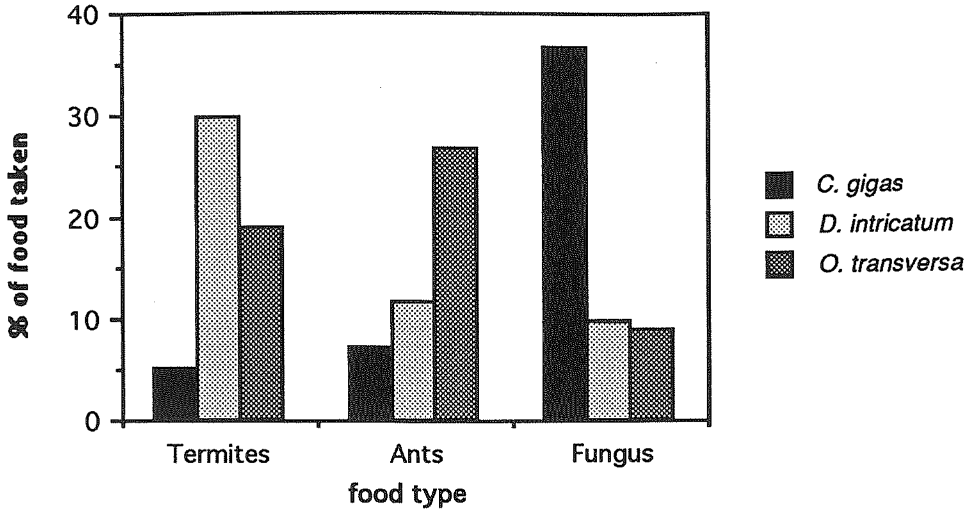


Fig. 5.4 shows the probability distribution of log food size classes consumed by the three species. It is approximately valid to assume that the food size distribution was continuous, and a close fit was found between the raw and model data. Resource widths and overlaps were calculated from this distribution.

Figs 5.5, 5.6 and 5.7 show the combined diel schedules for each species. All three species diel cycles differ. Four colonies' data are summed in each plot.

Fig. 5.4: Probability distribution of food size classes collected by the three ant species, constructed from the mean and standard deviation of the raw data.

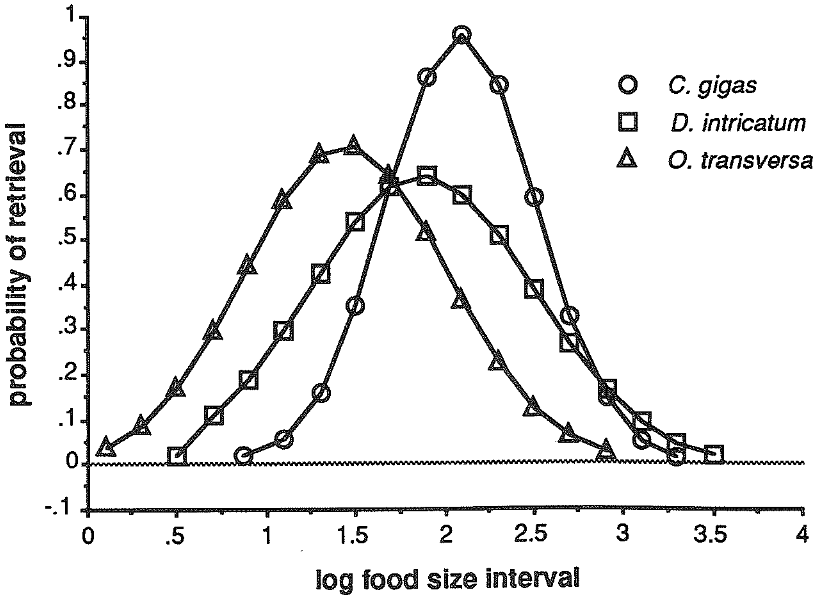


Fig. 5.5: *Camponotus gigas* diel schedule. This ant is primarily nocturnal.

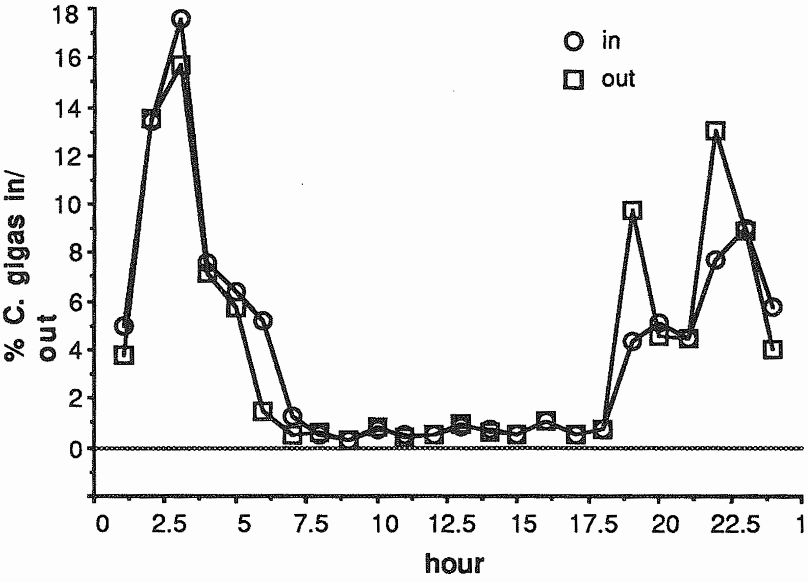


Fig. 5.6: *Diacamma intricatum* diel schedule. This ant is nocturnal and diurnal.

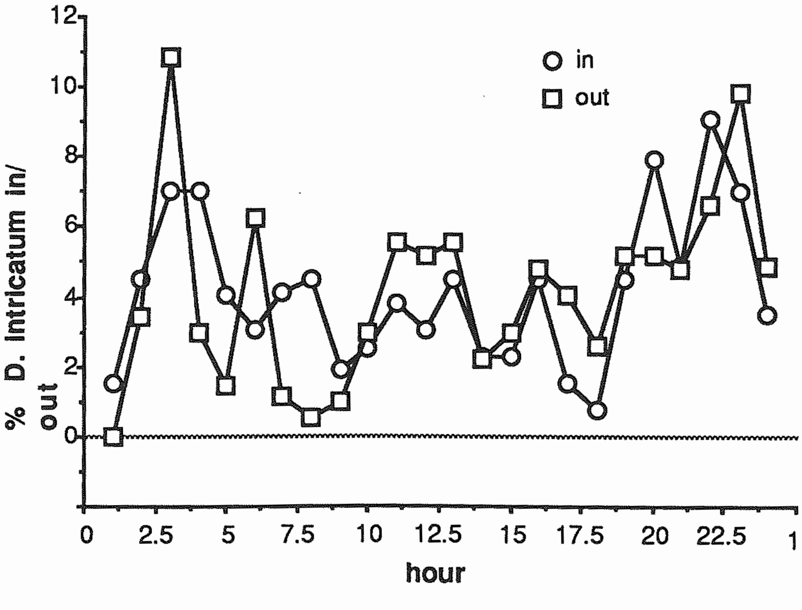


Fig. 5.7: *Odontoponera transversa* diel schedule. This ant is primarily diurnal.

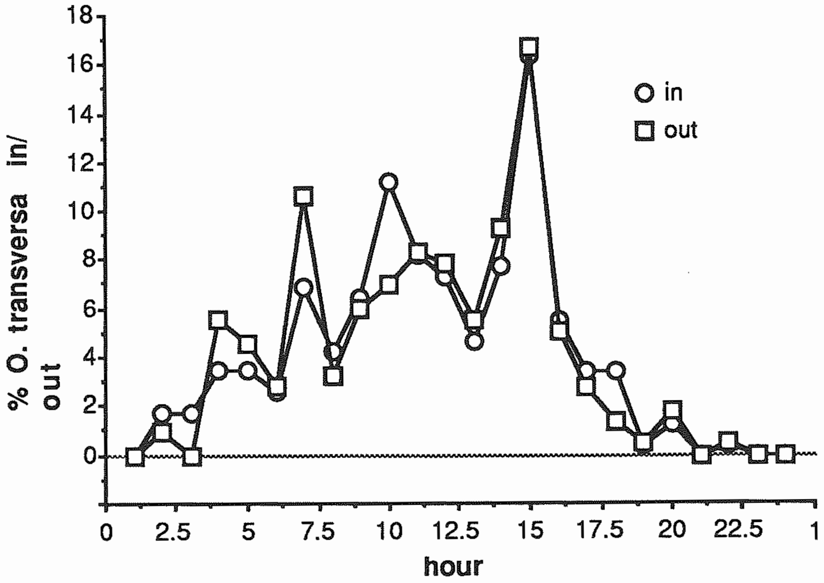


Table 5.4 shows Levins niche breadths for each species: *C. gigas* has the narrowest niche, and *D. intricatum* the widest.

Table 5.4: Levins niche breadths of three species, and mean percentage of total possible niche breadth.

species	food type	food size	foraging level: day/ night	time	mean % of total niche breadth
C. gigas	4.1	6.8	1.1, 1.4	1.2	39.6
D. intricatum	6.8	10.9	1.1, 1.2	1.9	52.0
O. transversa	7.1	9.9	1.0, 1.0	1.4	44.2

Table 5.5 shows percentage resource overlaps, mean percentage overlaps and overall multiplicative overlaps for the three two species interactions. Greatest niche overlap is between *C. gigas* and *D. intricatum*.

Table 5.5: Percentage resource overlaps for three species pairs, with mean overlaps and overall multiplicative overlaps for each species pair.

species pair	food type	food size	foraging level: day/ night	time: in, out	mean % overlap	overall % overlap
C. gigas/ D. intricatum	54.7	76.2	99.4, 91.8	72.7, 69.3	77.4	29.48
C. gigas/ O. transversa	44.5	50.28	96.8, 84.4	23.4, 24.3	53.9	5.33
D. intricatum/ O. transversa	70.4	71.5	97.5, 92.6	50.7, 55.0	73.0	26.12

Discussion

Tobin (1991) proposes that because ants are such a high proportion of the animal biomass in Neotropical forests, their trophic role must be more one of primary consumers than the carnivores they are usually held to be. This is in opposition to Sudd and Franks' (1987) statement that ants are primarily carnivores: it is given some support by my study, which showed that *C. gigas* consumes largely plant matter and detritus. The trophic roles of other ants in this habitat should be examined. The three species I examined may also have foraged for sugar from plants or bugs, for example, but my method of collection of food did not reveal this. All three responded to carbohydrate baits (chapter four), but it would not be possible to use data from this bait survey in combination with the collected forage, as it is not possible to say that resource availabilities are the same.

I found that observed nearest neighbour nest distances were overwhelmingly smaller than expected in the case of *D. intricatum* and *O. transversa*, indicating positive association, clumping, of their colonies. No other significant relationships were found. The only significant relationship at baits, between *C. gigas* and *O. transversa*, was also positive: this may be because resource overlap is lowest for *C. gigas* and *O. transversa*, and highest for *C. gigas* and *D. intricatum*. These two species' nest distributions tended non-significantly towards avoidance. The high resource overlap between *C. gigas* and *D. intricatum* might be viewed as surprising as they are in different subfamilies. The evidence for any pattern of association correlating with niche overlaps in these species is slight. Positive association relationships may reflect habitat preferences in foraging area, or responses to competitive pressure from other aggressive species, although this possibility is not supported by chapter four.

The resource creating most difference in species' overall resource overlap in this study is time. Time is known to be an important factor allowing ecological segregation in ant communities (Hölldobler and Wilson, 1990), often depending on physiological tolerance limits of species involved. Time segregation is likely to reduce interference competition between species, as opposed to food type or size, which reduces exploitative competition (Putman, 1994). *C. gigas*' primarily nocturnal habit reflects that of many other *Camponotus* species (personal observations).

All three species are relatively large, compared with other ants in the community, but *C. gigas* is the largest and *O. transversa* the smallest. Mean food size collected is distributed as expected from rank of body size.

Although negative interspecific competitive interactions have usually been found between ant species of higher abundance and social organisation, these three species apparently form an ecologically distinct guild of their own, that of large, ground dwelling, generalist solitary foragers. It is not clear whether such a group of species would be expected to compete interspecifically, but as Savolainen and Vepsäläinen (1988) note, within the broad hierarchy of the Finnish taiga ant community, each tier is further subdivided into further hierarchical tiers which compete amongst themselves.

The old problem that species differ in their resource utilisation whether they are under competitive pressure or not (Giller, 1984), occurs in this study. A null model would be needed to test whether the realised niches of these species are random or not. An improvement would be to have heeded May (1975) and to have calculated multidimensional resource overlap directly, by creating a single resource spectrum of all combinations of food type, food size, time and space variables. It would then be possible to avoid the problems of estimating multidimensional overlap indices indirectly, by adding or multiplying unidirectional measures, as I have done. However, in the complicated environment of a tropical rain forest, this is easier said than done. It might be possible with the use of specially designed baits, administered at prescribed times and places (e.g. Lynch et al., 1980), but might also lose important qualitative information, about food type for example.

Putman (1994) discusses the fundamental problems with studies like the present one. He notes that it must be shown first that resources are in fact in limited supply. This is notoriously difficult to establish in field studies, and is usually assumed, as I have done. However, resource limitation may in fact be of limited significance (Robert May, pers. comm.). Another problem is non-independence of resource axes. I found, on analysing data collected for this study, dependence only of space and time utilisation, and combined these into a single parameter. Resource type may also segregate species in different ways: differential utilisation of certain resources may influence potential for interference competition (e.g.space and time), or for exploitation competition (e.g. food type and size): models of resource partitioning are invariably assembled to examine exploitative competition. Diffuse competition from the rest of the community may also alter the effect individual species have on each other. He concludes that characterisation of niche parameters is useful primarily as a decscriptive tool of an organism's role in a community (its original function), and in fact has little predictive power. Abrams (1990) has proposed that ecological and evolutionary effects on the resource utilisation distributions of species may oppose each other, so that the resulting niche relations are difficult to interpret.

All three species are frequently found in the community: they are distributed quite evenly over the hectare and at all other sites I visited. They are obviously able to coexist adequately with this magnitude of resource overlap. The next step in understanding the dynamics of the relationships between these species would be to perform resource and colony density manipulation experiments, and to look at resource utilisation responses and fitness of the species as a result.

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CHAPTER SIX

Discussion: how is the Brunei rain forest ant community structured?

A search of Biological Abstracts for the first half of 1994 found 4420 papers on birds and 275 papers on ants. On communities there were 68 papers involving birds and 13 papers on ants. If insects account for most animal species and ants are 50% of the insect biomass world-wide (Wilson, 1990), it becomes clear that ants are being severely neglected, particularly as they are active in communities at all trophic levels, forming important ecological links (Gilbert, 1980), especially in tropical rain forests, perhaps the most threatened biome in the world.

Ant community diversity and distribution

Two different sampling methods showed that ants are the most numerically dominant taxon in the litter layer in this habitat. This result disagrees with most other tropical studies of community composition of the litter, but is in agreement with one other study in Borneo. It appears that Borneo is particularly rich in ants, although a comparison of the main sampling methodologies, Winkler extraction, Berlese extraction and hand sorting, is necessary to establish the effect of sampling methodology, and to make the study comparable with others.

I found 232 species in the litter and low vegetation layer using five sampling methods. Litter extraction yielded the highest number of species out of four sampling methods used. A model predicting the asymptotic number of species for each sampling method showed that Winkler litter sampling requires the fewest sampling units to accumulate 95% of all species it will find, and has the highest percentage of species unique to it. Pitfall sampling and vegetation hand sampling also have high numbers of species unique to them. Bait sampling does not, but may be used profitably to investigate interactions of species found in other sampling methods: it is very similar in species composition to vegetation and pitfall sampling. Searching for colonies in two 100 m^2 plots yielded seven new species, only 23% of all species found. This means that searching for colonies in the ground in this environment is one of the least efficient ways of accumulating species, bearing in mind the amount of time it took. For diverse tropical communities, it is simply not feasible (Alan Andersen pers. comm.). This result disagrees with Klimetzek and Pelz (1992) for central Europe.

Taxonomic differences were found in the vertical distribution of the fauna, Formicinae occurring more on vegetation, and Ponerinae on the ground. Ants were more abundant in the valley of the plot, and there was a borderline significant trend for higher species richness in the valley. The amount of litter sift, or small fragments of material in the valley was also higher, and best explained species richness. I propose that this component of the litter is important in providing nesting sites and foraging space for colonies, particularly those which nest in twigs as small as 3mm diameter, such as *Strumigenys* and tiny *Pheidole*.

Factors affecting the abundance of species of ants in the litter were primarily faunal, although it was difficult to assign significance values to individual cases. More of these interactions were positive than negative. The reason for this positive relationship is not clear. It may be caused by army or processional ants, *Leptogenys* or *Aenictus*, which reduce abundances of species to a low level where the have foraged- this reduces the potential for competition, maintaining diversity and making some samples which have not been raided richer in species which then appear to be positively associated. The species dwelling in tiny twigs may also be able to escape capture by the army ants who are unable to extract them from their small nest cavities. Some of these patterns have been documented for *Eciton*, by Franks (1982) and Franks and Bossert (1983) in tropical forests in Panama. Franks suggests that the regularly spaced foraging trails which these ants use maintain a constant state of ecological succession, and thus high diversity, in the litter.

Cryptic and specialist species were best sampled by litter extraction: most of the species foraging on the surface of the litter and plants are more generalist in their feeding habits, thus responding well to baits.

Colony dispersion patterns

Most of the non-random patterns found in the Brunei plots were positive, i.e. nest entrances tended, if anything, to be clumped within species or subfamilies. This result may be due to microhabitat preferences. Also, patterns tended to be more pronounced in plot 1, which was more densely populated. These results may be predicted in part by the models discussed, but the high risk of multiple nest entrances, or even polydomy (in which nests are split into several parts and found in different, and possibly non-adjoining locations) remains high, and largely confounds meaningful interpretation of the data, without further knowledge of the biology of the species.

Reanalysis and further investigation into a similar study by Levings and Franks (1982) showed that firstly, they had included in their analysis a species which is known to be unicolonial, so that any overdispersed pattern cannot realistically be ascribed to intraspecific competition, and secondly, that failure to remove edge effects in their analysis has led to a spurious finding of overdispersion. Their review paper (Levings and Traniello, 1981), is thus likely to be fundamentally statistically flawed, implying that spatial evidence of competition, at least in the way that they have interpreted it, needs to be reassessed for ant communities.

Foraging strategies and behavioural interactions

There was little evidence of any dominance hierarchy in the generalist surface foraging community in this forest: no direct negative interactions were found between groups of species of higher abundance, or between higher abundance and lower abundance species. Species of higher abundance did not cause other species to persist less at baits than species of low abundance, and were not less negatively affected by the presence of other species. They did not cause a decrease in overall species numbers where they occurred. However, more abundant species did persist more, and arrive faster at baits on trees, matching patterns found in the Finnish taiga biome (Savolainen and Vepsäläinen, 1988). Trees and higher quality baits were found to attract species at higher abundances, although no qualitative difference in species was found (but see above).

Although it was only possible to show that three species were solitary foragers due to sample sizes, modal abundances of all species suggest that this foraging strategy is prevalent in the litter layer, and moderate recruitment is commonest on the trees. Two of the three solitary foragers were found to forage less successfully in the presence of other species.

Subfamilies differed significantly in modal abundance and persistence on the ground, with Dolichoderinae the most abundant and persistent. This subfamily is primarily arboreal, and may have been attracted from the trees to the ground baits, although I have seen it feeding on palm fruits at nearly ground level.

Temporal patterns gave the best support for a dominance hierarchy scenario of the type found by Fellers (1987) and Savolainen and Vepsäläinen (1988): subfamilies differed in the time of occurrence and persistence, suggesting avoidance by less abundant species, especially *Odontoponera transversa*, of species of higher abundance which occurred and/or persisted more later. Manipulative experiments would illuminate the direction of causation of these interactions. These temporal patterns were not strongly reflected by diversity changes over time. Species-rank abundance plots showed weakly the opposite pattern to the Berger-Parker diversity index: the former showed decreased evenness over time, and the latter decreased numerical dominance by *Odontoponera transversa*. i.e. increased evenness.

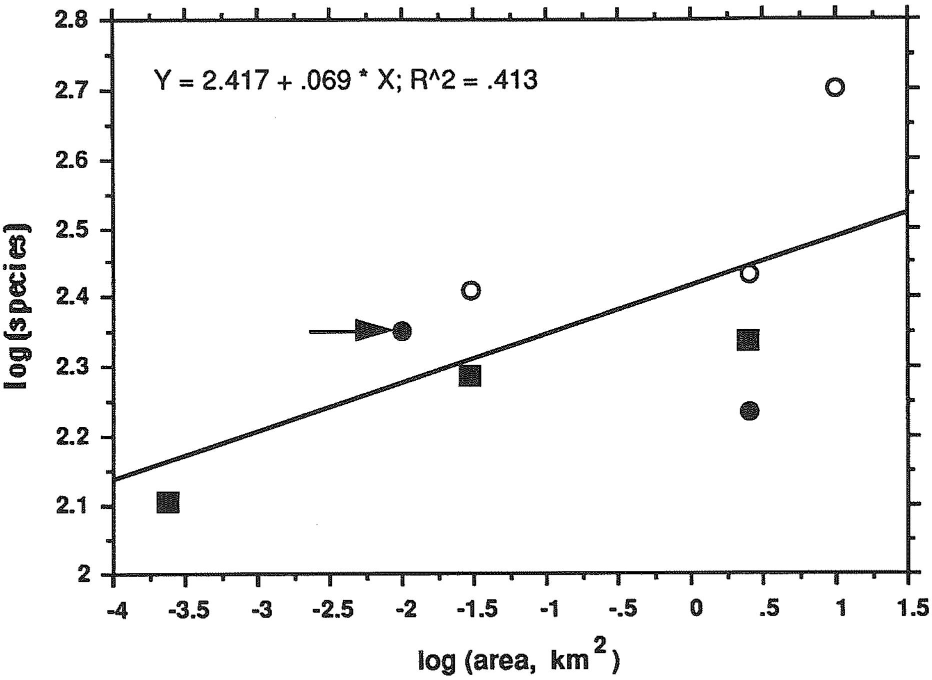
Interspecific colony dispersion and niche relations of three large tropical rain forest ant species

Nests of *Odontoponera transversa* and *Diacamma intricatum* were closer together than expected, possibly indicating a microhabitat preference effect. Resource overlap between *Odontoponera transversa* and *Camponotus gigas* was lowest, and their association at baits positive. *Camponotus gigas* and *Diacamma intricatum* overlapped most in resources, and their nests were non-significantly negatively associated. I have not calculated a d/w ratio (distance apart of means/standard deviation of utilisation distribution) for these species as I have combined several unidirectional axes: calculating this ratio would illuminate their precise overlap and make the system comparable to other communities. In any case overall overlap is not particularly high for any pair of species. If the resources are considered separately, however, food type/ size overlap is quite high for all pairs of species. Segregation is strongest in the time axis, although not between species of the greatest food overlap. If absolute limits do exist for the overlap of sympatric species (MacArthur and Levins, 1967), then it is useful as a descriptive tool to measure the actual overlap of all axes of a species resource use to describe this, whether these axes are naturally different or diverge in order to reduce competition between species. It is then easy to test which axes are affected by competition and how much, depending on external competitive forces.

Synthesis

The number of species which I found in this forest fits with other workers' findings, when area is accounted for (fig. 6.1).

Fig. 6.1: Simple regression of log (species number) against log (area in km^2) of ants in tropical forests and plantations (for data see chapter two). Closed points = Old World, open points = New World, circles = primary forest, squares = includes plantation or secondary forest. p=0.0001. My result is indicated by an arrow.



Although numbers of studies are small, New World studies fall on or above the line, and Old World below it, except in my case which falls above the line. However, Chung's (1993) Bornean study falls below the line, as do all studies including areas of plantation or secondary forest. More data is necessary to test whether biogeographic factors, forest degradation or methodology best explain differences in diversity found in these studies.

The role of microhabitat effects and nest site availability in these communities should be investigated more seriously, by offering artificial nest sites as in Franks (1982), for example. Franks also noted the important role of army ants in depressing numbers and maintaining diversity of ants in the litter. This deserves further attention in the Old World (Egbert Leigh, pers. comm.).

Two spatial dispersion studies used to predict community processes were not found to be very productive or easy to interpret in this habitat. The method has in the past been plagued with at least two sorts of statistical bias caused by edge effects and non-independence, and suffers from lack of sufficient understanding of the population biology and colony structure of the species in the tropics. I would not recommended these methods as preliminary descriptors of tropical ground ant communities, until the species biology is better known.

The overall evidence for a competitive hierarchy in the litter and low vegetation ant community from this study is very poor. In most cases where a non-random pattern of species association has occurred at ground level, I have been able to suggest an explanation involving alternative microhabitat or environmental factors. The behavioural patterns which are clearest are often on vegetation. This may be because of the food resources here, as suggested by Jackson (1984). Traniello (1989) notes that *Formica schaufussi* occurs in increased abundances at carbohydrate baits. This at first appears to contradict my own findings, but the explanation is that this species habitually uses honeydew as a food resource and recruits to it because it is renewed: scattered invertebrate prey are renewed less predictably, and the species does not recruit to them so well. The species in the litter community are overall less likely to use sugar as a resource than are the vegetation-foraging species, and my finding that abundances fall from tree to ground carbohydrate baits support this. Thus the trophic roles of species on the vegetation are likely to be somewhat different on the whole from those in the litter, where carnivory and scavenging reign. This in turn affects the level of recruitment to food items on the trees and ground, and, potentially, the level of aggression and strength of interspecific interactions.

However, my results are consistent with the predictions of May (1973). Species interactions are weak and species numbers are high. Whether the numbers of interactions per species remains constant, as predicted, cannot at present be established as the entire competition matrices are known for few, if any, ant communities. I did not establish definite interactions between any pair of species, only that overall they tend to be weak. Looking for interactions within and between genera rather than apparent guilds, as I have done, may be the next step in establishing whether species are competing. Closely related are in theory more likely to compete, as their ecological requirements will be more similar. The genera *Polyrhachis* and *Camponotus* would be particularly suitable for investigation of this, as they are often ground nesting, and their large body size makes them easy to mark. They are also both Formicinae and quite closely related.

Illumination of the roles of species which in this study occurred at baits with high abundance, such as *Dolichoderus*, *Crematogaster* and *Philidris*, in other habitats such as secondary forests, plantations and other primary forest types, such as heath forest, would be useful: In primary dipterocarp forest, their high abundance had no special negative effect on other species or each other, apparently due to their infrequency in the habitat. This in fact made their role quite hard to test, but strong effects would not, in any case, be expected at low densities. Wilson's (1990) assertion that impoverishment leads to dominance would seem to be true: potentially dominant species do not depress foraging success of other species more than do species of low abundance. The costs to these species of extirpating others, in this habitat, may to be too high. Comparative studies of their effects on other species in less speciose habitats would clarify these phenomena.

The next step in establishing what 'structure' exists in the ground and litter community, and how it is maintained, should focus on the roles of nest site availability and army ant predation, and possibly even the relationship between these two factors. More comparison of tree and ground competitive and trophic patterns and are needed. It is important to establish, finally, to what degree ants can be considered trophic generalists.

Andersen (1990) recommends ants as bio-indicators of land restoration processes in Australia, because they are diverse and abundant in all habitats; they are functionally important at all trophic levels and integrate a wide variety of biotic and abiotic variables; they are easily sampled and processed; they are sensitive to environmental change, and respond rapidly to that change. I propose that the use of ant communities as indicators of forest recovery should be investigated in South East Asia: as previously mentioned, forests in this region are under severe threat, and the abundance of ants on Borneo would make them ideal candidates for biological indicators, if we can find out how community patterns change across successional and degraded habitats.

It is surprising that tropical ant community structure is not better known: as mentioned in the introduction, ants are a model taxon for testing community theory, yet, for their biomass, curiously little is known of their biology, particularly in the tropics. Strong patterns in the Old World have been described for species in less than ten genera. With the rapid demise of the world's tropical rain forest, establishing the ecological role of the ants must surely be of prime importance.

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APPENDIX: Chapter 2

species no.	subfamily	genus	tree bait	ground bait	litter	pitfall	vegetation
50	Dolichoderinae	*Dolichoderus*	1	1			1
51	Dolichoderinae	*Dolichoderus*	1	1			1
52	Dolichoderinae	*Dolichoderus*	1	1			1
60	Dolichoderinae	*Dolichoderus*					1
55	Dolichoderinae	*Lowriella**		1		1	
54	Dolichoderinae	*Philidris*	1	1		1	
56	Dolichoderinae	*Tapinoma*		1			
57	Dolichoderinae	*Technomyrmex*	1	1	1	1	
59	Dolichoderinae	*Technomyrmex*					1
156	Dorylinae	*Dorylus*				1	
203	Dorylinae	*Dorylus*				1	
64	Dorylinae	*Aenictus*					1
200	Formicinae	*Acropyga*			1		
201	Formicinae	*Acropyga*			1		
1	Formicinae	*Camponotus*	1	1	1	1	1
4	Formicinae	*Camponotus*	1	1			1
5	Formicinae	*Camponotus*	1	1			
13	Formicinae	*Camponotus*	1	1			1
14	Formicinae	*Camponotus*	1	1	1		1
16	Formicinae	*Camponotus*	1	1			1
18	Formicinae	*Camponotus*	1	1		1	1
9	Formicinae	*Camponotus*				1	
10	Formicinae	*Camponotus*		1			
6	Formicinae	*Camponotus*					1
8	Formicinae	*Camponotus*					1
11	Formicinae	*Camponotus*					1
12	Formicinae	*Camponotus*					1
15	Formicinae	*Camponotus*					1
17	Formicinae	*Camponotus*	1				1
241	Formicinae	*Camponotus*					1
61	Formicinae	*Cladomyrma*					1
19	Formicinae	*Echinopla*		1			1
20	Formicinae	*Echinopla*					1
21	Formicinae	*Echinopla*	1	1			1
23	Formicinae	*Euprenolepis*	1	1		1	
22	Formicinae	*Euprenolepis*					1
198	Myrmicinae	*Myrmoteras*			1		
199	Formicinae	*Myrmoteras*			1		
301	Formicinae	*Myrmoteras*			1		
24	Formicinae	*Paratrechina*	1	1		1	1
25	Formicinae	*Paratrechina*	1	1	1	1	1
27	Formicinae	*Paratrechina*	1	1			
26	Formicinae	*Paratrechina*		1	1	1	
28	Formicinae	*Paratrechina*		1	1	1	
290	Myrmicinae	*Paratrechina*		1	1	1	
202	Formicinae	*Plagiolepis*			1		
29	Formicinae	*Polyrhachis*	1	1			1
30	Formicinae	*Polyrhachis*		1			1
32	Formicinae	*Polyrhachis*		1	1		1
33	Formicinae	*Polyrhachis*		1	1	1	1
34	Formicinae	*Polyrhachis*	1	1			1
35	Formicinae	*Polyrhachis*	1	1	1		1
36	Formicinae	*Polyrhachis*	1	1			1
39	Formicinae	*Polyrhachis*	1	1			1
40	Formicinae	*Polyrhachis*	1	1	1		1
42	Formicinae	*Polyrhachis*		1		1	1
31	Formicinae	*Polyrhachis*					1
37	Formicinae	*Polyrhachis*					1

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* This genus was described by Steve Shattuck on the basis of having seen specimens collected in the Kuala Belalong reserve.

38	Formicinae	*Polyrhachis*	1				1
41	Formicinae	*Polyrhachis*					1
43	Formicinae	*Polyrhachis*					1
44	Formicinae	*Polyrhachis*					1
45	Formicinae	*Polyrhachis*					1
46	Formicinae	*Pseudolasius*			1	1	
48	Formicinae	*Pseudolasius*			1		
49	Formicinae	*Pseudolasius*			1	1	
53	Formicinae	*Pseudolasius*				1	
158	Myrmicinae	*Acanthomyrmex*		1	1		
159	Myrmicinae	*Acanthomyrmex*				1	
116	Myrmicinae	*Anillomyrma*				1	
160	Myrmicinae	*Aphaenogaster*		1	1	1	
114	Myrmicinae	*Calyptomyrmex*			1		
115	Myrmicinae	*Calyptomyrmex*				1	
162	Myrmicinae	*Cardiocondyla*		1	1		1
161	Myrmicinae	*Cataulacus*	1			1	
163	Myrmicinae	*Crematogaster*	1	1	1	1	
164	Myrmicinae	*Crematogaster*	1	1		1	1
167	Myrmicinae	*Crematogaster*	1	1			1
168	Myrmicinae	*Crematogaster*		1			1
174	Myrmicinae	*Crematogaster*	1	1			
179	Myrmicinae	*Crematogaster*	1	1		1	1
180	Myrmicinae	*Crematogaster*	1	1			
176	Myrmicinae	*Crematogaster*				1	
165	Myrmicinae	*Crematogaster*	1				1
166	Myrmicinae	*Crematogaster*					1
169	Myrmicinae	*Crematogaster*					1
171	Myrmicinae	*Crematogaster*	1				
172	Myrmicinae	*Crematogaster*	1				
173	Myrmicinae	*Crematogaster*					1
175	Myrmicinae	*Crematogaster*					1
177	Myrmicinae	*Crematogaster*					1
87	Myrmicinae	*Dilobocondyla*					1
113	Myrmicinae	*Eurhopalothrix*			1		
181	Myrmicinae	*Lophomyrmex*		1	1	1	
112	Myrmicinae	*Lordomyrma*				1	
182	Myrmicinae	*Meranoplus*			1		
194	Myrmicinae	*Monomorium*					1
192	Myrmicinae	*Monomorium*		1	1	1	1
195	Myrmicinae	*Monomorium*				1	1
191	Myrmicinae	*Monomorium*			1		
190	Myrmicinae	*Monomorium*					1
193	Myrmicinae	*Monomorium*					1
108	Myrmicinae	*Myrmecina*			1		
109	Myrmicinae	*Myrmecina*			1		
183	Myrmicinae	*Myrmicaria*				1	
300	Myrmicinae	*Oligomyrmex*		1	1	1	1
205	Myrmicinae	*Pheidole*		1	1	1	1
204	Myrmicinae	*Pheidole*		1	1	1	
206	Myrmicinae	*Pheidole*			1		
209	Myrmicinae	*Pheidole*		1	1	1	
210	Myrmicinae	*Pheidole*			1		
211	Myrmicinae	*Pheidole*				1	
212	Myrmicinae	*Pheidole*			1		
214	Myrmicinae	*Pheidole*				1	
215	Myrmicinae	*Pheidole*		1			
216	Myrmicinae	*Pheidole*		1			
234	Myrmicinae	*Pheidole*		1	1		
235	Myrmicinae	*Pheidole*			1		
236	Myrmicinae	*Pheidole*			1		
237	Myrmicinae	*Pheidole*			1		
238	Myrmicinae	*Pheidole*				1	
208	Myrmicinae	*Pheidole*	1	1	1	1	

223	Myrmicinae	*Pheidole*	1	1	1	1	
240	Myrmicinae	*Pheidole*		1	1		
220	Myrmicinae	*Pheidole*			1		
221	Myrmicinae	*Pheidole*			1		
226	Myrmicinae	*Pheidole*	1	1			1
227	Myrmicinae	*Pheidole*	1	1	1	1	
231	Myrmicinae	*Pheidole*	1	1			
224	Myrmicinae	*Pheidole*		1	1	1	
225	Myrmicinae	*Pheidole*		1	1	1	
228	Myrmicinae	*Pheidole*				1	
229	Myrmicinae	*Pheidole*		1	1	1	
230	Myrmicinae	*Pheidole*				1	
219	Myrmicinae	*Pheidole*					1
250	Myrmicinae	*Pheidole*	1		1	1	
233	Myrmicinae	*Pheidole*		1		1	
270	Myrmicinae	*Pheidole*	1				
185	Myrmicinae	*Pheidologeton*	1	1	1	1	
184	Myrmicinae	*Pheidologeton*		1	1		
186	Myrmicinae	*Pheidologeton*				1	
110	Myrmicinae	*Pristomyrmex*			1		
111	Myrmicinae	*Pristomyrmex*			1		
187	Myrmicinae	*Proatta*			1	1	
188	Myrmicinae	*Recurvidris*		1			
189	Myrmicinae	*Recurvidris*		1		1	
84	Myrmicinae	*Smithistruma*				1	
85	Myrmicinae	*Smithistruma*			1		
86	Myrmicinae	*Smithistruma*			1		
70	Myrmicinae	*Strumigenys*	1		1		
79	Myrmicinae	*Strumigenys*	1		1		
65	Myrmicinae	*Strumigenys*			1		
66	Myrmicinae	*Strumigenys*			1		
67	Myrmicinae	*Strumigenys*			1		
68	Myrmicinae	*Strumigenys*			1		
69	Myrmicinae	*Strumigenys*			1	1	
72	Myrmicinae	*Strumigenys*			1		
73	Myrmicinae	*Strumigenys*			1		
74	Myrmicinae	*Strumigenys*			1		
75	Myrmicinae	*Strumigenys*			1		
76	Myrmicinae	*Strumigenys*			1		
77	Myrmicinae	*Strumigenys*			1		
78	Myrmicinae	*Strumigenys*			1		
80	Myrmicinae	*Strumigenys*			1		
81	Myrmicinae	*Strumigenys*			1	1	
82	Myrmicinae	*Strumigenys*			1	1	
83	Myrmicinae	*Strumigenys*			1		
71	Myrmicinae	*Strumigenys*					1
92	Myrmicinae	*Tetramorium*		1			1
102	Myrmicinae	*Tetramorium*	1	1		1	1
88	Myrmicinae	*Tetramorium*		1	1	1	
89	Myrmicinae	*Tetramorium*			1	1	
90	Myrmicinae	*Tetramorium*			1		
93	Myrmicinae	*Tetramorium*			1		
94	Myrmicinae	*Tetramorium*			1	1	
95	Myrmicinae	*Tetramorium*			1		
96	Myrmicinae	*Tetramorium*			1	1	
97	Myrmicinae	*Tetramorium*				1	
99	Myrmicinae	*Tetramorium*				1	
100	Myrmicinae	*Tetramorium*			1	1	
101	Myrmicinae	*Tetramorium*			1	1	
103	Myrmicinae	*Tetramorium*					1
106	Myrmicinae	*Vollenhovia*				1	1
104	Myrmicinae	*Vollenhovia*			1		
117	Ponerinae	*Anochetus*		1			
118	Ponerinae	*Anochetus*			1		

119	Ponerinae	*Anochetus*			1	1	
120	Ponerinae	*Cerapachys*				1	
121	Ponerinae	*Cerapachys*			1		
122	Ponerinae	*Cerapachys*			1		
123	Ponerinae	*Cerapachys*			1		
135	Ponerinae	*Cryptopone*				1	
2	Ponerinae	*Diacamma*		1	1	1	
125	Ponerinae	*Gnamptogenys*	1	1	1	1	
126	Ponerinae	*Gnamptogenys*			1		
127	Ponerinae	*Gnamptogenys*			1		
128	Ponerinae	*Gnamptogenys*					1
129	Ponerinae	*Harpegnathos*			1	1	
130	Ponerinae	*Hypoponera*			1	1	
131	Ponerinae	*Hypoponera*			1		
132	Ponerinae	*Hypoponera*			1		
133	Ponerinae	*Hypoponera*			1		
136	Ponerinae	*Leptogenys*				1	
137	Ponerinae	*Leptogenys*				1	
138	Ponerinae	*Leptogenys*				1	
139	Ponerinae	*Leptogenys*				1	
140	Ponerinae	*Leptogenys*				1	
141	Ponerinae	*Leptogenys*		1	1	1	
142	Ponerinae	*Leptogenys*		1		1	
143	Ponerinae	*Leptogenys*		1		1	
157	Ponerinae	*Myopias*			1		
144	Ponerinae	*Mystrium*				1	
145	Ponerinae	*Odontomachus*			1		
3	Ponerinae	*Odontoponera*		1	1	1	
146	Ponerinae	*Pachycondyla*			1	1	
147	Ponerinae	*Pachycondyla*			1		
148	Ponerinae	*Pachycondyla*				1	
149	Ponerinae	*Pachycondyla*			1	1	
150	Ponerinae	*Pachycondyla*		1	1	1	
152	Ponerinae	*Ponera*				1	
153	Ponerinae	*Ponera*			1	1	
154	Ponerinae	*Ponera*			1		
155	Ponerinae	*Ponera*				1	
62	Pseudomyrmecinae	*Tetraponera*					1
63	Pseudomyrmecinae	*Tetraponera*	1				1

APPENDIX: Chapter 4

				glp			gsp			gc			tlp			tsp			tc		
list order	species no.	subfamily	genus	points	mean ab.	modal ab.	points	mean ab.	modal ab.	points	mean ab.	modal ab.	points	mean ab.	modal ab.	points	mean ab.	modal ab.	points	mean ab.	modal ab.
1	50	Dolichoderinae	*Dolichoderus*	3	4.33	4	3	3.79	4	2	2.14	2	3	4.25	4	3	4.17	4	2	1.67	2
2	51	Dolichoderinae	*Dolichoderus*	3	3.33	3	3	3.17	3				1	1	1	1	1	1			
3	52	Dolichoderinae	*Dolichoderus*	4	4	5	5	3.92	4				3	3.4	3	3	3.4	3			
4	55	Dolichoderinae	*Lowriella*	1	4.4	4	1	4	4												
5	54	Dolichoderinae	*Philidris*	5	4.46	5	6	4.08	5	1	2	2	5	4.35	5	4	4.78	5			
6	56	Dolichoderinae	*Tapinoma*				1	3	3	1	1	1									
7	57	Dolichoderinae	*Technomyrmex*	5	2.33	3	4	2.5	2	4	2.8	2	1	3	2	1	3	3			
8	200	Formicinae	*Acropyga*				1	2	2												
9	1	Formicinae	*Camponotus*	78	1.2	1	61	1.1	1	38	1.12	1	2	1.5	1	3	1	1	6	1	1
10	4	Formicinae	*Camponotus*	3	2.44	3	3	1.5	1				4	2.85	3	3	2.92	3			
11	5	Formicinae	*Camponotus*	3	2.63	4	3	2.33	1				1	4	4	1	3.33	3			
12	10	Formicinae	*Camponotus*	1	1	1															
13	13	Formicinae	*Camponotus*	3	1	1	2	1	1	3	1	1	2	1.25	1	1	2	2			
14	14	Formicinae	*Camponotus*	2	1	1				1	1	1	3	2.13	3	3	2	1	2	2	2
15	16	Formicinae	*Camponotus*	1	3.5	3	1	1	1				4	3.43	4	4	3.07	3	1	1	1
16	17	Formicinae	*Camponotus*										1	3	3						
17	18	Formicinae	*Camponotus*	1	1	1	1	1.5	1	1	1	1	5	2.46	3	6	2.29	2	2	2	1
18	19	Formicinae	*Echinopla*							1	2.5	2									
19	21	Formicinae	*Echinopla*	1	2	2							1	1	1				1	1	1
20	23	Formicinae	*Euprenolepis*	3	2.2	2	1	2	2	2	1.67	2	1	3	3	2	2.5	2	1	3	3
21	24	Formicinae	*Paratrechina*	2	2	1	2	2.75	3	2	2	2	3	3.33	3	2	2	2	1	4	4
22	25	Formicinae	*Paratrechina*	13	2	2	11	2	2	13	2.09	2	9	2.67	2	5	2	1	3	3.25	3
23	26	Formicinae	*Paratrechina*	4	2.11	2	8	1.94	2	8	2.1	2									
24	27	Formicinae	*Paratrechina*	1	2.67	3	2	2	1	1	1	1				1	3	3	1	3	3
25	28	Formicinae	*Paratrechina*	6	2	2	2	3	2	2	1.5	1									
26	290	Formicinae	*Paratrechina*	1	2	2	1	1	1												
27	202	Formicinae	*Plagiolepis*										1	3	3	1	3	3			
28	29	Formicinae	*Polyrhachis*	1	1	1	1	1	1	1	1	1							1	1	1
29	30	Formicinae	*Polyrhachis*	1	2	2															
30	32	Formicinae	*Polyrhachis*							1	1	1									
31	33	Formicinae	*Polyrhachis*	12	1.06	1	8	1	1	17	1.04	1									
32	34	Formicinae	*Polyrhachis*	4	1.6	1	4	1	1	4	1	1	2	2	1	1	3	3			
33	35	Formicinae	*Polyrhachis*	6	1.13	1	4	1	1	3	1	1				2	1	1	2	1.5	1
34	36	Formicinae	*Polyrhachis*	1	1	1							2	1	1						
35	38	Formicinae	*Polyrhachis*										3	1	1	1	1	1	1	1	1
36	39	Formicinae	*Polyrhachis*	3	2.64	3	5	1.92	1	2	1.75	1	8	2.42	3	7	2.58	3	1	1	1
37	40	Formicinae	*Polyrhachis*	6	2.71	3	7	1.94	1	4	1	1	6	2.85	3	6	2.63	3	1	2	2

38	42	Formicinae	*Polyrhachis*	1	1	1	1	1	1	1	1	1									
39	158	Myrmicinae	*Acanthomyrmex*	1	1.5	1				1	1	1									
40	160	Myrmicinae	*Aphaenogaster*	4	1	1	4	1	1	1	1	1									
41	162	Myrmicinae	*Cardiocondyla*	1	2	2	5	1.43	1												
42	161	Myrmicinae	*Cataulacus*										1	2	2				1	3	3
43	168	Myrmicinae	*Crematogaster*	1	3.6	4															
44	174	Myrmicinae	*Crematogaster*	1	4.75	5	2	2.8	3	1	2	2	2	2.8	3						
45	167	Myrmicinae	*Crematogaster*	2	3.73	3	3	2.93	3				3	4.14	5	3	3.17	4	1	2.5	2
46	163	Myrmicinae	*Crematogaster*	3	3.11	3	4	3.36	4	1	1	1	3	3.5	3	2	3.75	4	1	3	3
47	179	Myrmicinae	*Crematogaster*	3	3.33	4	3	2.9	3				6	2.76	3	5	2.72	3			
48	180	Myrmicinae	*Crematogaster*	3	4.08	5	3	3.5	4	1	2	2	2	3.89	5	2	4.14	5	1	1	1
49	164	Myrmicinae	*Crematogaster*							1	1	1	1	4.25	5				1	3.2	3
50	165	Myrmicinae	*Crematogaster*										1	1	1	1	3.33	3	1	4	3
51	171	Myrmicinae	*Crematogaster*										1	3	3						
52	172	Myrmicinae	*Crematogaster*										1	5	5	1	5	5			
53	181	Myrmicinae	*Lophomyrmex*	11	1.92	1	10	2.13	2	5	2.43	3									
54	192	Myrmicinae	*Monomorium*	4	3.2	3	6	2.29	2												
55	300	Myrmicinae	*Oligomyrmex*	3	2.5	2	3	2.67	3												
56	205	Myrmicinae	*Pheidole*	1	2	2	4	2.29	2												
57	208	Myrmicinae	*Pheidole*	1	2	2										1	1	1			
58	209	Myrmicinae	*Pheidole*	1	2	2	3	2	2	1	3	3									
59	224	Myrmicinae	*Pheidole*	1	2.67	1	1	3.2	3	1	2	2									
60	225	Myrmicinae	*Pheidole*	1	1.5	1	1	2	2	1	2	2									
61	226	Myrmicinae	*Pheidole*	1	3	3							1	4	4	1	2.2	2	1	3	3
62	231	Myrmicinae	*Pheidole*	1	1	1				1	4	4	1	3	3	1	2	1			
63	233	Myrmicinae	*Pheidole*	1	3	3	1	2	2												
64	234	Myrmicinae	*Pheidole*	1	2	2	1	1	1	1	2	2									
65	229	Myrmicinae	*Pheidole*	4	2.95	3	4	2.56	2	2	2	2									
66	223	Myrmicinae	*Pheidole*	15	2.42	3	11	2.15	2	9	1.9	1	9	2.9	3	7	2.67	3	1	2.67	3
67	204	Myrmicinae	*Pheidole*	21	2.11	2	22	2.31	2	12	1.75	1									
68	227	Myrmicinae	*Pheidole*	22	2.55	2	23	2.05	1	18	1.59	1				1	2.5	2			
69	216	Myrmicinae	*Pheidole*				1	3	3	1	2	2									
70	240	Myrmicinae	*Pheidole*				1	4	4	1	2	2									
71	250	Myrmicinae	*Pheidole*										1	3	3	1	2	2			
72	270	Myrmicinae	*Pheidole*													1	3	3			
73	184	Myrmicinae	*Pheidologeton*	1	4	4	1	2	2	1	1	1									
74	185	Myrmicinae	*Pheidologeton*	3	4.38	5	3	4.08	4	1	3	2	1	5	5	2	4.43	4			
75	189	Myrmicinae	*Recurvidris*	1	2	2	1	2.5	2	1	3	3									
76	188	Myrmicinae	*Recurvidris*				1	2	2												
77	70	Myrmicinae	*Strumigenys*										2	3.6	4	2	3.8	4			
78	79	Myrmicinae	*Strumigenys*										1	2.33	2	1	2.5	2			

79	102	Myrmicinae	*Tetramorium*	3	2.14	1	2	2.75	3				2	2.17	2	2	1.5	1			
80	88	Myrmicinae	*Tetramorium*				1	1	1												
81	92	Myrmicinae	*Tetramorium*				1	1	1	1	1	1									
82	117	Ponerinae	*Anochetus*	1	1	1															
83	2	Ponerinae	*Diacamma*	42	1.02	1	31	1.03	1	33	1	1									
84	125	Ponerinae	*Gnamptogenys*	4	1.7	1	6	2	1	2	1.5	1	6	2.06	2	4	2.38	2	2	2.6	3
85	141	Ponerinae	*Leptogenys*	14	2.53	3	17	2.11	3	1	1	1									
86	142	Ponerinae	*Leptogenys*	2	3.75	4	1	3	3												
87	143	Ponerinae	*Leptogenys*				1	5	5												
88	3	Ponerinae	*Odontoponera*	128	1.37	1	115	1.3	1	52	1.18	1									
89	150	Ponerinae	*Pachycondyla*	32	1.24	1	28	1.16	1	7	1.13	1									
90	63	Pseudomyrmecinae	*Tetraponera*										1	2	2						
	NUMBER OF SPECIES			67			64			50			43			40			24		
	MEAN ABUNDANCE			2.34			2.23			1.64			2.82			2.69			2.22		
	MEAN ABUNDANCE SD			1.05			0.98			0.71			1.08			1.02			1.01		
	MEAN ABUNDANCE SE			0.13			0.12			0.10			0.16			0.16			0.21		