Seasonal and Spatial Patterns in Ground Foraging Ants in a Rain Forest in the Western Ghats, India[1]

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ABSTRACT

Seasonal variation and spatial distribution in ground foraging rain forest ants were studied in South Kannada–Kodagu District in Karnataka (India) between 1990 and 1991 by pit-fall trap sampling. All ant species showed marked seasonality. A total of 31 species were recorded from the primary forest over a period of two years. More species were recorded from the closed canopy forest than from tree fall gaps in primary forest. All ant species showed marked seasonality with fewer species and individuals sampled/plot during the wetter seasons. The numerically dominant species, *Pheidole* sp,. was markedly lower in abundance during the wet seasons. Spatial patterns were also studied during a dry season both in the primary forest and an adjacent logged forest. More species were recorded from the logged forest than the primary forest. Community composition in primary forest was different from that in logged forest. Common species were more ubiquitous than rarer species. Species were distributed bimodally across sampling plots. Probable underlying processes behind these seasonal and spatial patterns have been discussed.

Key words: ground foraging ants, India, logged forest, rain forest, seasonal fluctuation, spatial pattern, Western Ghats.

THE ROLE OF SPATIAL AND TEMPORAL PATTERNS at the population and ecosystem level have recently been emphasized in ecology (Levin 1992). More information is needed on the small scale distribution of species and the effects of seasonality on tropical communities to understand the processes underlying the generation and maintenance of species diversity (Levings 1983).

Ants play an important role in the dynamics of tropical rain forests both in terms of abundance and biomass, and in ecological processes such as nutrient cycling, energy turnover, pollination, seed dispersal, and seed predation (Greenslade & Greenslade 1984, Andersen & Ashton 1985, Andersen 1987, Andersen & Majer 1991, Gomez & Zamora 1992). Because of their ubiquitous distribution, dominance and ease of experimental manipulation, ants have been used as model organisms for understanding the patterns and processes underlying ecological communities (Andersen 1990, Levings & Franks 1982). Work on tropical rain forest ant communities in the Old and New Worlds has been carried out by Levings (1983), Wilson (1959, 1987), Andersen (1991a, 1992), Torres (1984a, b), Brown (1973) and Room (1971, 1975).

Although about 650 species of ants are known

from the Indian sub-continent (Bingham 1903), little is known of their ecology. The present study, carried out on the ground foraging ant community in a rain forest in the Western Ghats (India), attempts to answer the following questions about seasonal and spatial patterns: 1) What is the local species diversity of ground foraging ants in this rain forest and is it comparable to that in other tropical forests at the same latitude? 2) Do forager populations of different ant species and the community structure as a whole undergo seasonal changes? Does rainfall influence seasonal fluctuations? 3) Does the diversity and composition of the ground foraging ants vary between the closed canopy forest and natural tree fall gaps within a single primary forest habitat? Does the diversity and composition of ground foraging ants in primary forest vary from that in a logged forest in the same region in a given season? 4) How are species distributed within a habitat?

STUDY SITE

The study area, near Uppungala, is in the Western Ghats, near the boundary between Dakshina Kannada and Kodagu Districts in the Karnataka State (12°32'35"N, 75°40'22"E) at an altitude of 350 to 400 m (Fig. 1). This region has 4 to 5 dry months with an average annual rainfall between 3000 to 3500 mm (Pascal 1982). December to March were considered as dry, April and May as early wet, June to September as wet, with
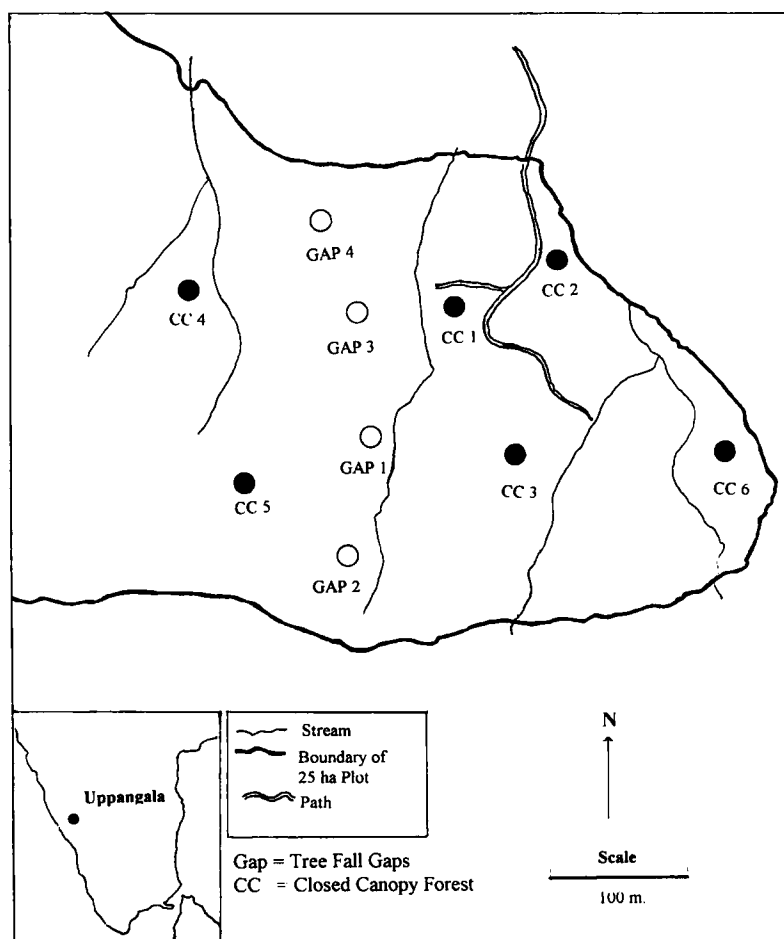
FIGURE 1.   Map showing the study area and the locations of different sampling plots in the primary forest.

October and November being considered as late wet season (Fig. 2).

The underlying geological formation in this area is an archean to proterozoic complex of migmatites and grandioritic to tonalitic gneisses (Ferry 1992). Following the French classification, the soil is described as highly desaturated and poor ferralitic (Ferry 1992). He also described soil at the depth of 0–10 cm as moist, deep brown with fine litter debris. Standing crop of litter on the forest floor is at maximum in April–May (Ferry 1992). The study was conducted in a primary low elevation evergreen forest of *Dipterocarpus-Kingiodendron-Humboldtia* type (Pascal 1988) from January 1990 to November 1991. Besides *Dipterocarpus indicus* and *Kingiodendron pinnatum*, the other dominant tree species was *Vateria indica* with *Humboldtia brunonis* as an understorey tree (Pascal 1988). Studies at the primary forest were

conducted both under closed canopy and in tree fall gaps. Tree fall gaps had early successional vegetation (B. R. Ramesh, pers. comm.). The temperature variation at the tree fall gaps was more than that in the closed canopy forest (pers. obs.). In addition, a site in an adjacent logged/burnt (hereafter referred to as the 'logged site') forest, located at an altitude of 300 to 350 m, was chosen for the study. The logged site dominated by pioneer species was selectively logged between 1974–75 to 1982–83 (Loffeier 1988). It was burned in the 1980s. The logged site with its regenerating vegetation was floristically different from the primary forest and in some parts about 80 percent of the individuals (>10 cm girth) were *Macaranga peltata* (Loffeier 1988). Diurnal temperature variation in the logged forest was about 20°C (Loffeier 1988) which was considerably greater than that in the primary forest (pers. obs.). The canopy
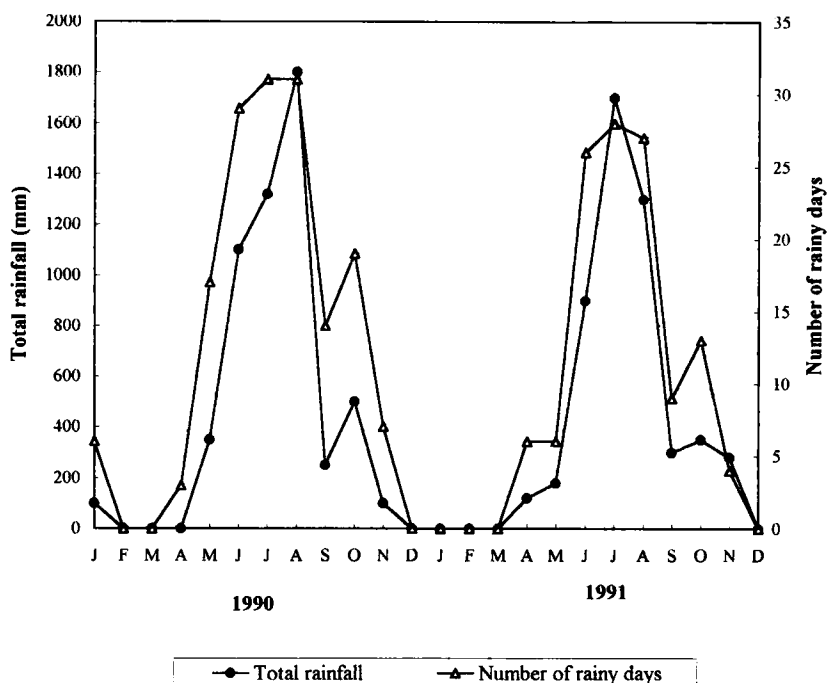
FIGURE 2.   Total rainfall/month (mm) and number of rainy days/month for 1990–1991 recorded at Kolumuguru (approximately 10 km from the study area).

in the logged site was distinctly more open than the closed canopy primary forest (pers. obs.).

MATERIALS AND METHODS

Pit fall traps were used to sample the ants (Donnelly & Giliomee 1985; Koch & Majer 1980; Samways 1981, 1983, 1990; Levings 1983; Romero & Jaffe 1989; Andersen 1991a, b). Pitfall trapping is a sampling method which is easily standardized and replicated in space and time, however it can only give relative estimates of populations. The efficacy of pitfall traps in sampling forest ants has been questioned (Olson 1991).

PRIMARY FOREST.—Sampling was carried out at the primary forest site using pitfall traps (10 plots, each 10 m × 10 m), avoiding rocky substratum and steep slopes. Six plots were located under closed canopy forest and four in tree fall gaps. All the plots were at the same elevation (±30–50 m). Sampling was conducted in both dry and wet seasons. All plots were sampled once a month in each sampling season.

LOGGED FOREST.—Pitfall sampling was carried out

in 4 plots (10 m × 10 m) at the logged site. Three of these plots were at the same altitude and were approximately 100 m apart. The fourth plot was located 40 m lower and about 0.5 km away from the other plots. Plots in the logged site were sampled during early March to May in 1991.

LOCATION OF TRAPS.—Twenty-five traps were placed uniformly (with approximately 1.5 m gap between two traps) in each of the 100 square meter plots. Each trap was a plastic can (25 cm long × 8 cm diameter) placed in a hole dug in the soil. The edge of the trap was flush with the soil surface and $\frac{1}{5}$ of each trap was filled with detergent solution as a killing agent. Traps were collected after 24 hr. During the rainy months, each trap was provided with a cover placed 10 cm above the mouth of the trap to prevent rain water from entering.

All species were identified to morpho-species (identifications were confirmed by Dr. T. M. Ali at the University of Agricultural Science at Bangalore). Poor taxonomic knowledge of Indian ants (B. Bolton, pers. comm.) did not allow us to be certain about the species. Wherever species level identification was not possible, the species was identified to genus and a species code assigned to it. This was often the case with a few genera belonging to sub-

family Myrmicinae. Some error in estimating the forager population of these genera is thus likely.

All data were log(x + 1) transformed before statistical analysis. Data for both years were compared using t-test to check if the number of species and the average number of individuals in the pitfall traps per plot, at a given season, differed significantly.

Variation in the number of species and number of individuals trapped from each plot (pooled seasonally for both years) over four seasons were analysed using one way ANOVA. Rarefaction analysis was done to compare the species richness between the closed canopy and the treefall gap plots at the primary forest site (Ludwig & Reynolds 1988). Rank-abundance of different species for different seasons was analysed using pooled data (for all plots and years). To keep points (abundance of different species against the rank) from colliding with each other, they were located randomly on a short vertical axis using SYSTAT statistical package (Wilkinson 1990).

Abundance of a species in a season was averaged for all the plots. Coefficient of variation (standard deviation/mean) for each species over different seasons was calculated and was then regressed with abundance of different species. Species diversity was measured as the Shannon-Weiner diversity index, denoted by $H' = -\Sigma\ p_i \log p_i$, where p_i = proportion of each species in the community. Evenness in the community was measured by a modified Hill's evenness index, i.e., $1/((\text{Simpson's index}) - 1)$, Simpson's index $= \Sigma\ p_i^2$. For the period March 1991 through May 1991, similarity among plots at the primary and the logged forest sites was examined using single linkage cluster analysis (Wilkinson 1990).

The Morisita-Horn Index was used to estimate the similarities among various plots in the primary and the logged forest (Gadagkar et al. 1990). This index is denoted by $2\Sigma\ (an_i \cdot bn_i)/(da + db)aN \cdot bN$, where aN = total number of individuals in plot A and an_i = number of individuals in the ith species in plot A. $da = \Sigma\ an_i^2/aN^2$).

RESULTS

PRIMARY FOREST.—Thirty-one species, representing 24 genera, were collected in primary forest (in closed canopy and tree fall gaps) from an overall catch of 32,621 individuals over different seasons and years. An average of 21.8 species and 3262.2 individuals were caught per plot. *Leptogenys* was the most species rich genus (3 species). *Pheidole, Cre-*

TABLE 1. *Relative abundances (proportion) of each species of ants in the primary forest (pooled from ten plots and from all seasons in 1990–1991) N = Number of individuals sampled.*

Species	N	Proportion
Pheidole sp. 1	10,321	0.4038
Tetramorium tortuosum	3087	0.1208
Crematogaster wroughtoni	2780	0.1088
Monomorium sp. 1	2184	0.0854
Aphaenogaster beccarii	1823	0.0713
Tetramorium sp. 2	1625	0.0636
Monomorium sp. 2	1187	0.0464
Oecophylla smaragdina	627	0.0245
Pheidologeton sp.	397	0.0155
Pheidole sp. 2	300	0.0117
Camponotus sp. 1	285	0.0112
Leptogenys sp. 1	176	0.0069
Strumigenys sp.	168	0.0066
Odontomachus sp.	115	0.0045
Paratrechina sp.	108	0.0042
Crematogaster sp. 2	97	0.0038
Leptogenys sp. 2	88	0.0034
Bothroponera sp.	62	0.0024
Aenictus aitkenii	34	0.0013
Diacamma vagans	23	0.0009
Odontoponera sp.	12	0.0005
Leptogenys sp. 3	9	0.0004
Camponotus compressus	9	0.0004
Myopias sp.	9	0.0004
Mesoponera sp.	6	0.0002
Ectatomma sp.	6	0.0002
Platythyrea victoriae	5	0.0002
Tapinoma melaniformis	5	0.0002
Harpegnathus saltator	4	0.0002
Amblyopone belli	4	0.0002
Pseudoponera sp.	3	0.0001

matogaster, Monomorium, Tetramorium and *Camponotus* were represented by 2 species each (Table 1). Most of the species were found during the first seven sampling months (including dry and wet seasons), while the species accumulation curve plateaued after the tenth month. *Pheidole* sp. 1 was the overall dominant species in the sample pooled from different seasons and sampling plots (40.38% of the total) (Table 1).

Thirty-one species from 21 genera were recorded from plots in the closed canopy forest. Twenty-six species from 18 genera were recorded from plots in tree fall gaps. Rarefaction analysis showed species richness to be higher in the closed canopy forest than that in the gap forest (Fig. 3).

SEASONAL VARIATION.—There was no significant variation in the number of species per plot (species number/100 m²) and the average number of individuals per plot between years for any given season. Data for both years were hence pooled to ex-
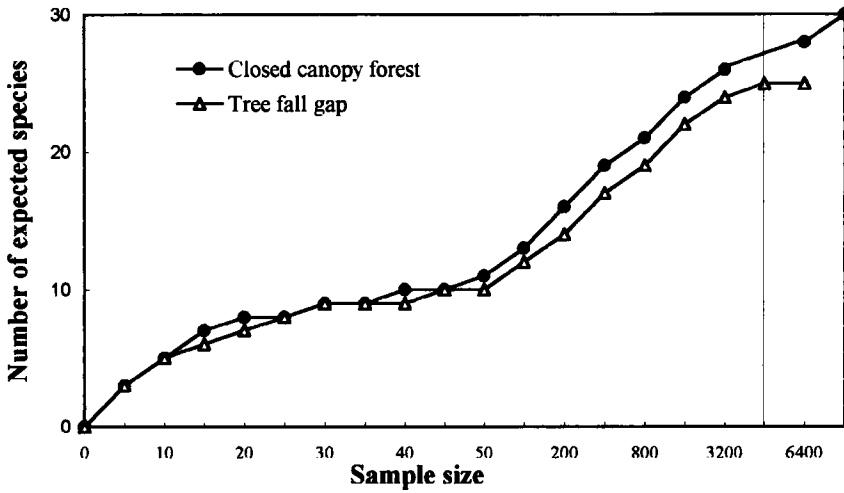
FIGURE 3.   Comparison of species richness in the closed canopy and tree fall gaps using the rarefaction method.

amine seasonal variations. Species number/plot varied significantly between seasons (Table 2). Species number/plot was highest during the dry season and fell sharply as the monsoon progressed, and was lowest during the late wet season (Fig. 4a). Total number of individuals sampled/plot also varied significantly over seasons (Table 2). The seasonal fluctuation of the number of individuals/plot followed the same pattern as the number of species (Fig. 4b). There was a positive correlation between the number of species and the number of individuals in the sample ($r = 0.55$, $N = 117$, $P < 0.001$).

Community composition also changed considerably over the seasons. Species number was highest during the dry season (29 species) and progressively lower during the early wet season (27 species), the wet season (19 species) and the late wet season (13 species). Interestingly, the evenness in the community was lower in the dry season (despite a high

TABLE 2.   *ANOVA table showing variance in number of species and number of individuals over seasons.*

Source	SS	MSS	df	F
Number of species				
Between	0.587	0.196	3	72.109*
Within	0.098	0.0027	36	
Number of individuals				
Between	9.367	3.122	3	17.714*
Within	6.346	0.176	36	

Note: SS = Sum of squares, MSS = Mean sum of squares, df = Degrees of freedom.
* = $P < 0.001$.

species number), as compared to the wet season which can be attributed to a low species diversity index in dry months (Table 3). This phenomenon can be attributed to the domination of the community by a few species during the dry season as compared to wet season.

Rank-abundance plots (Fig. 5a–5d) clearly demonstrate the changes in the position of the dominant species in the community. There was a total change in the dominant species composition from dry to late wet season. While *Pheidole* sp. 1 was the most abundant species (43.41%) during dry season, it dropped to second place (21.1%) during the late wet season. *Monomorium* sp. 1 became the most abundant species during the late wet season. Evenness in the community increased with the drop in abundance of *Pheidole* sp. 1. The positions of other species next to *Pheidole* sp. 1 with regard to abundance status shifted at different seasons. *Monomorium* sp. 1 showed the most striking change in abundance over seasons. Its abundance varied from 1175 (6.49% of season's total) during the dry season to 673 (12%) during early wet and 132 (4%) during wet season which increased sharply to 290 (22%) during the late wet season.

Average abundance of different species was negatively correlated with their temporal variability (measured as coefficient of variation of the abundance of different species over seasons) ($R^2 = 0.753$, $N = 31$, $P < 0.001$) (Fig. 6).

SPATIAL PATTERNS.—Five species, *Amblyopone belli*, *Aenictus aitkenii*, *Pseudoponera* sp., *Mesoponera* sp.
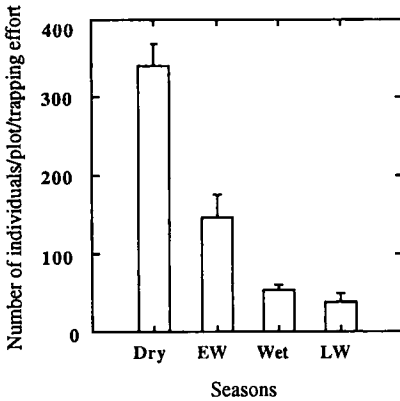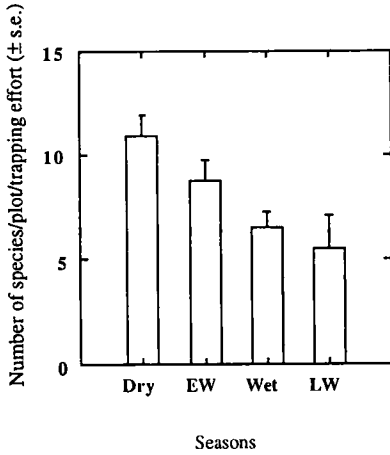
FIGURE 4.   Seasonal fluctuation in a) the mean number of species (±SE) (per 100 m² per trapping effort) and b) mean number of individuals (±SE) (per 100 m² per trapping effort) using data pooled for both years. EW = early wet, LW = late wet.

TABLE 3.   *Species diversity and community evenness measures for different seasons at the primary forest site (pooled for all the plots).*

	Seasons			
	Dry	Early wet	Wet	Late wet
S	29	27	19	13
$e^{H'}$	5.58	7.82	5.96	7.29
Modified Hill's evenness index	0.47	0.63	0.64	0.68

Note: S = Number of species, H' = Shannon Weiner's diversity index, Modified Hill's evenness index = $1/(Sp_i^2)/e^{H'} - 1$.

COMPARISON OF PRIMARY FOREST WITH LOGGED FOREST.—A total of 36 species was recorded in pitfall traps from all the plots including the primary (both closed canopy and tree fall gaps) and logged forests during early March to early May 1991. Twenty-nine species were recorded from the primary forest site during this period. Of these, 24 species were recorded from the plots in the closed canopy forest and 27 species were recorded from the tree fall gaps. Thirty-one species from 21 genera were found from plots at the logged site during the same period.

Plots in the primary and logged forest were compared for the period from March to May 1991 (dry season) using Morisita-Horn index of similarity. Single linkage clustering on the similarity indices distinctly separated the plots in the closed canopy forest (Plots 1 to 5) from those in the tree fall gaps in primary forest (Plots 7 to 10) and the logged forest (Fig. 7). Plot 6 in the closed canopy forest, however, clustered with the plots in the tree fall gaps in primary forest site and the logged site.

SPECIES DISTRIBUTION.—The species distribution was bimodal. When ten pit fall trap plots in the primary forest were considered (including both closed canopy and natural tree fall gaps) out of 31 species, only 8 were present only in one to two plots. Seven species were present in 3 to 5 plots and 12 species were present in 7 to 10 plots (Fig. 8).

The abundant species were found in a larger number of plots than the rarer ones. This was apparent when the relative abundance of different species was plotted against the number of plots within which each species was found (Fig. 9). There was a positive correlation between relative abundance and the number of plots within which each species was found at the primary forest ($R^2 = 0.80$, $N = 31$, $P < 0.001$).

and *Diacamma vagans*, were recorded only from the plots in closed canopy forest, while *Platytheria victorae* was recorded only from 2 plots in the tree fall gaps. Species richness, diversity measure and evenness at different plots in the primary forest are shown in Table 4. These values were calculated for each plot from pooled data for all seasons.

LOGGED FOREST.—In the logged forest, 31 species from 21 genera were recorded. Four species: *Crematogaster* sp. 3, *Leptothorax* sp., *Monomorium* sp. 3, and *Pheidole* sp. 5 were recorded exclusively in the logged site plots.
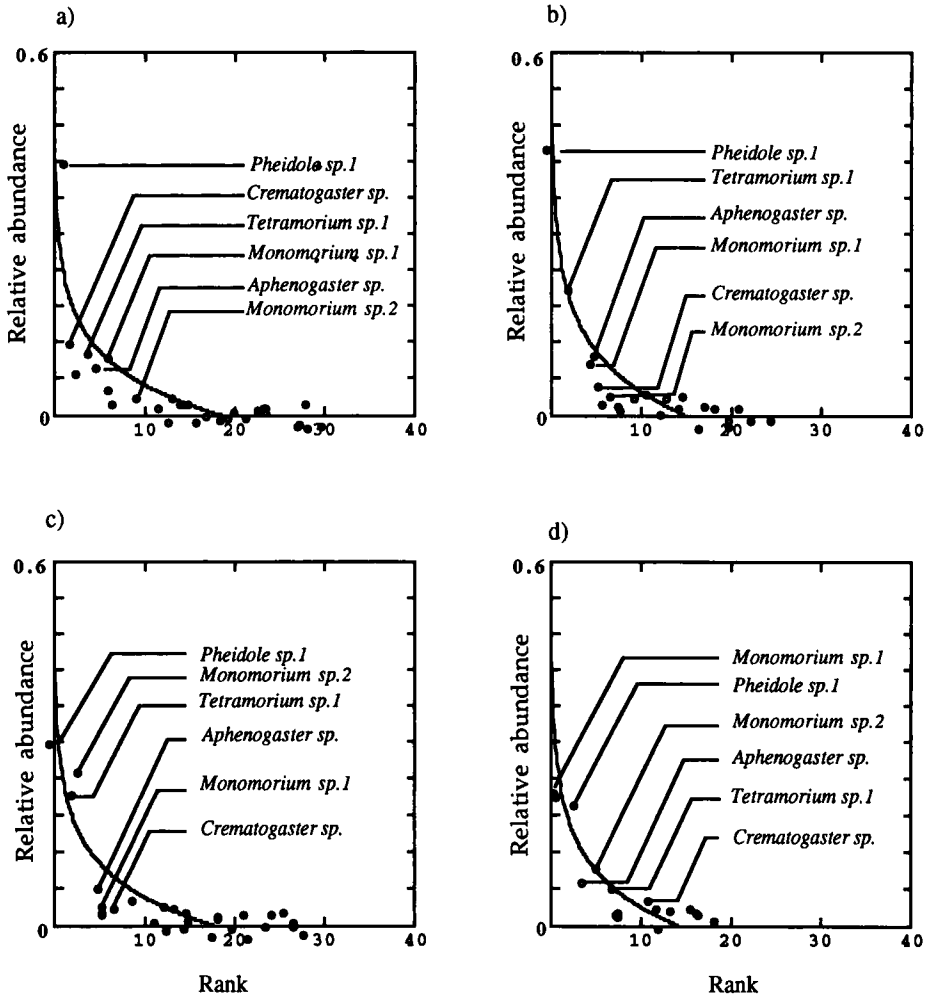
a)

b)

c)

d)

FIGURE 5.   Species rank-abundance curves for different seasons in the primary forest plots (data pooled from all plots and sampling years). To keep points from colliding they were jittered slightly. Fit in the plot is logarithmic. a) Dry season, b) early wet season, c) wet season and d) late wet season.

DISCUSSION

LOCAL SPECIES DIVERSITY AND DENSITY.—Very little is known about the local species density and diversity of ant fauna from the Indian sub-continent. The only available account comparable to the study is an unpublished work by R. Gadagkar *et al.* (pers. comm.) which gives an estimate of local ant species diversity in a region in the Western Ghats. Although the present study was restricted to the ground foraging ant fauna, the finding supports their estimate of 13 to 33 ant species per habitat, ranging from plantation to primary forest, which they sampled. Neither of the estimates comes close to the much higher estimates of local ant species

diversity observed in the Neotropics exemplified by the studies by Wilson (1959, 1987), Levings and Windsor (1985), Majer and Queiroz (1990) and Verhaagh (1990). Unfortunately, very few accounts are available comparing local diversities of the Old and the New World ant fauna. Carroll (1979) showed Liberian (West Africa) local diversity to be much lower than that in Costa Rica. Tree canopies have been shown to be species poor in Africa (Room 1971) and in Australia (Andersen 1986a, Majer 1990). Floristic diversity has also been found to be low in the Western Ghat forests compared to the Neotropics and even to Malaysian forests (Pascal 1988). Daniels *et al.* (1992) showed the Western Ghats to be impoverished in bird species di-
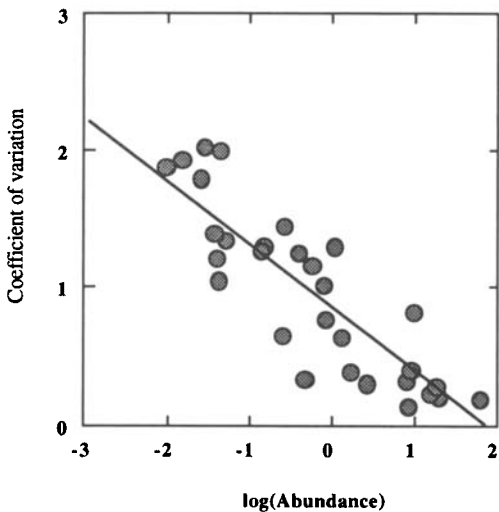
FIGURE 6. Seasonal variability (co-efficient of variation) of different species in the primary forest in relation to their respective log(x + 1) transformed abundances.
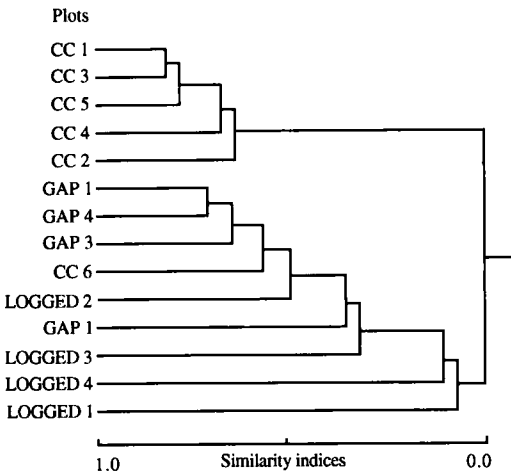

FIGURE 7. Dendrogram showing the similarities among different plots at the primary and logged forest sites during the dry season in 1991. Index of similarity is Morisita-Horn's similarity index. CC 1 to 6 = closed canopy plots in primary forest site, GAP 7 to 10 = natural tree fall gaps in primary forest, LOGGED 1 to 4 = plots in the logged forest.

versity. Raven and Axelrod (1974) attributed the overall biotic impoverishment of this region to plate tectonic movements. However, more comparative studies on different taxonomic groups are required across geographical gradients before a general explanation emerges for this phenomenon.

SEASONAL PATTERN.—The study has shown strong seasonal fluctuations within the ant community. There were significant variations in total ant abundances from the dry to the wet season. The rank-abundance curves, used for visualizing dominance patterns in the community (Samways 1983, Begon *et al.* 1990), showed dominance by *Pheidole* sp. 1 during the dry season. This pattern changed in the wet season with *Monomorium* sp. 1 becoming dominant. The community also became more even in the wet season. Seasonal cues like the dry and rainy period are well known to affect tropical insect community structure (Wolda 1978, 1989; Levings & Windsor 1985) and ants also follow this pattern

(Andersen 1983, 1986a, b; Greenslade & Greenslade 1984; Davidson 1977). Ant abundance was higher during the dry season in a Peruvian lowland forest (Pearson & Derr 1986) and in an Amazonian rain forest in Brazil (Adis & Schubert 1984, Adis 1988). In temperate regions cold conditions inhibit ant activity and a distinct summer-winter activity cycle is visible in ant communities of this region (Herbers 1989, Holldobler & Wilson 1990). Cold desert ants show a prominent winter inactivity and a spring activity cycle (Davidson 1977; Bernstein 1974, 1979; Whitford 1978). Some species are restricted by the extreme summer and have a short period of activity in spring (Davidson 1977, Whitford 1978). On the basis of his study on the cicadas in Panama, Wolda (1989) questioned rainfall as the causal factor behind seasonality in the tropical insects. Levings and Windsor (1985) noted that arthropod populations of a tropical deciduous forest

TABLE 4. *Species diversity and evenness measures for each plot in the primary forest site. Plots 1 to 6: closed canopy forest, Plots 7 to 10: tree fall gaps.*

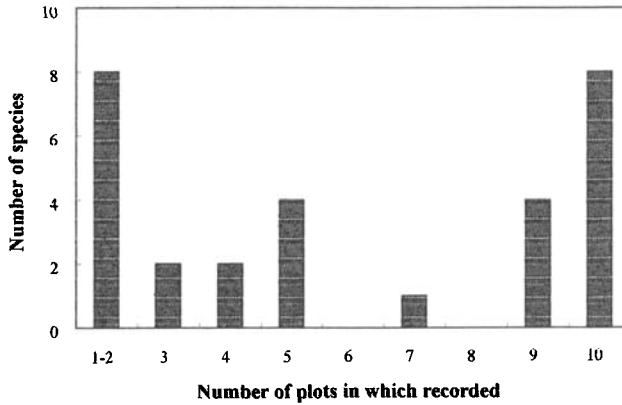|	Plots									
	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8	Plot 9	Plot 10
S	22	19	18	14	20	19	20	22	20	16
$e^{H'}$	9.12	7.14	9.13	2.23	7.33	6.02	8.43	9.66	4.72	7.23
Modified Hill's evenness index	0.71	0.65	0.79	0.36	0.59	0.58	0.77	0.76	0.67	0.81

FIGURE 8. Species frequency distribution among different plots at the primary forest site.

in Panama were low when there was a long wet season with heavy late wet season rainfall. Rainfall has been cited as a major factor in ant seasonality. As for the possible reason for this seasonal variability, seasonal pattern in ant activity can be attributed to seasonal changes in the brood cycle (Levings 1983, pers. obs.).

As apparent from the results, common species showed less variability than the rarer species. This can be attributed to the low forager densities of rarer species which made them vulnerable to strong seasonal changes. On the other hand, the common species could withstand environmental unfavourability like heavy rains owing to their higher forager density. Samways (1990) reported the same phenomenon in a sub-tropical ant community in

FIGURE 9.   Relation between number of individuals of a species caught in pitfall traps (log(x + 1) transformed) sampled from all plots in primary forest and the number of plots in which it is found. $R^2 = 0. 80$, $N = 31$, $P < 0.001$.

South Africa where populations of common species were less variable in time.

SPATIAL VARIATION.—Ants have often been reported to be patchily distributed within a single locality (Room 1971, 1975; Levings & Traniello 1981). The study showed the surface activity of the ground foraging ant community in the primary forest or more specifically, the community at the closed canopy primary forest varied from that in the logged forest site. Interestingly, the community in the natural tree fall gaps in the primary forest was more similar to that in the logged forest than the closed canopy primary forest site. Several factors like availability of moisture (Levings 1983, Levings & Windsor 1985), vegetation structure (Doncaster 1981; Andersen 1983, 1986b) and litter quality (Schowalter 1985) have been suggested as factors that might determine patchiness.

Although this study did not attempt to quantify the habitat characteristics, qualitative observations indicated that plots in the closed canopy primary forest site were distinctly different from those in the tree fall gaps and the logged site with regard to the various factors mentioned above. Structure of vegetation can directly affect ant activity in terms of the availability of nesting and foraging sites and modification of the microclimate. It can also have indirect influence through the supply of food (Greenslade 1971, Tilman 1978, Boring et al. 1981, Greenslade & Thompson 1981, Schowalter 1981, Greenslade & Halliday 1983, Andersen 1986a).

The substratum in the logged forest was also different from that in the primary forest in terms of the insolation and litter depth (qualitative ob-
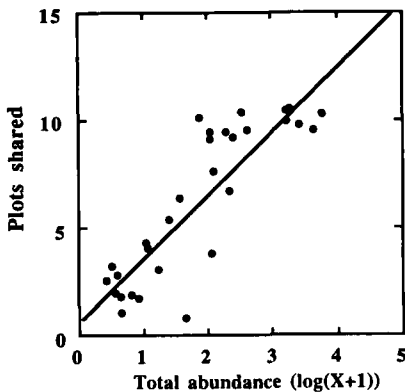
servation). On the other hand, the natural tree fall gaps in the primary forest and the logged area were more similar in terms of the above factors. Ants are known to be sensitive to fluctuations in surface temperature (Brian & Brian 1951, Pontin 1963, Room 1971, Carlson & Gentry 1973, Greenslade 1979). The substratum in the logged forest site and the tree fall gaps with their higher exposure to the sunlight had a higher temperature regime which could have also attributed to the difference in the ant community structure at the logged site from that at the primary forest site.

Santos and Whitford (1981) and Seastedt and Crossley (1981) reported enhancement in litter arthropod population growth following disturbance. Adis (1988) recorded more arthropod species from the secondary forest than primary forest in Amazonia.

SPECIES DISTRIBUTION.—The species distribution at different plots in the primary forest site in the study was clearly bimodal. One group of species occupied 90–100% of the plots while the other group occupied 10 to 20% of the plots. In the middle were the species with intermediate range of distribution occupying about 50% of the plots. This distribution is clearly in accordance with the distribution pattern predicted by Hanski (1982) in his 'core-satellite hypothesis' (a group of locally abundant core species inhabiting all suitable sites at one mode and a group of rare satellite species distributed randomly among different sites within

a habitat). Brown (1984) criticized Hanski's model saying it is an artifact of sampling scale. Collins and Glenn (1991) showed this hypothesis of bimodal species distribution to hold true even at a larger sampling scale.

The data showed a strong positive association between the abundance of a species and the number of plots it occupied. Association between abundance of ecologically similar species and their distribution (number of plots occupied in a single region) has been noticed in a variety of taxa since the last decade (Hanski 1982, Bock & Ricklefs 1983, Brown 1984, Collins & Glenn 1991). The present study shows this to be the case within a single habitat too. More abundant species shared more sampling plots in the primary forest habitat. Samways (1983) reported the similar phenomenon where more abundant species of ants shared more numbers of plots at a regional scale.

ACKNOWLEDGMENTS

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