ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/279890543

Soil and litter cryptic ant assemblages of Bahian cocoa plantations. Pedobiologia

ARTICLE in PEDOBIOLOGIA · JANUARY 1995

Impact Factor: 1.42

CITATIONS
18

READS
11

2 AUTHORS, INCLUDING:

Jacques H C Delabie

268 PUBLICATIONS 2,534 CITATIONS

SEE PROFILE

Available from: Jacques H C Delabie
Retrieved on: 16 January 2016

Pedobiologia 39, 423–433 (1995)
Gustav Fischer Verlag Jena

Soil and litter cryptic ant assemblages of Bahian cocoa plantations

Jacques H. C. Delabie[1] **and Harold G. Fowler**[2]

[1] Entomology, Cocoa Research Center (CEPEC), CEPLAC, C.P. 7, 45600 Itabuna, Bahia, Brazil
[2] Department of Ecology, Institute of Biosciences, UNESP, 13506-900 Rio Claro, São Paulo, Brazil

Summary. Soil cores and Berlese litter samples collected in an old cocoa plantation in the state of Bahia, Brazil, revealed high ant species richness and strong dominance. The A horizon soil stratum had twice as many species present (113) as the litter stratum (69), with true species richness estimated at 117 and 75, respectively. A total of 124 species were present in samples from the combined strata. Litter depth was not found to significantly affect litter ant species richness. The dominant litter ant species was *Solenopsis geminata medusa*, while the dominant A horizon soil species was *Acropyga* cf. *paramaribensis*. Species rank-order relationships of the two strata were not concordant. The effects of trophic specialization, microenvironments, and species interactions are discussed.

Key words: Ant, community, assembly, tropical forest, Brazil, structure

Introduction

The effects of ground ants on ecossystem function are extremely variable. Ants are generally considered beneficial for soils under agriculture or natural vegetation, due to predation of pests and the regulation of non-pest insect populations, as well as due to their nesting activities which promotes the mechanical incorporation of the superficial decomposing organic matter accelerating soil mineralization and inducing chemical and physical changes in the soil structure (Petal 1978). However, some soil ants can be considered pests in some circumstances, such as species of *Acropyga* which tend mealybugs on the roots of tropical tree crops (Borgmeier 1927; Bunzli 1935; Roba 1936; Weber 1944; Delabie 1990).
Little published information is available upon the ground ant fauna in tropical areas (Strickland 1945; Wilson 1959; Kempf 1961; Culver 1974; Greenslade & Greenslade 1977; Levings & Franks 1982; Levings 1983), in spite of the fact that ants are one of the dominant components of the ground fauna, both in terms of biomass and species richness (Fowler et al. 1991). In this paper, we examine the structure and inter-relations of litter and subterranean ant assemblages of a South American cocoa plantation. Our studies assemblages are defined as cryptic because of "activity confined to soil and litter" (Andersen 1987).

Materials and Methods

This study was performed in the Research Center of Cocoa, CEPLAC; in Ilhéus, State of Bahia, Brazil. The area is situated in the region of the South American Atlantic Forest, currently restricted to relict fragments. Climatic conditions are characteristic of the humid tropics, with two seasons, defined

Correspondence to: H. G. Fowler

principally by temperature variations rather than by irregular precipitation patterns. Sampling was conducted in an old cocoa plantation which had not received any chemical treatment over a 20 year period. Shade was irregular and consisted principally of 10 to 20 m tall secondary-growth trees. Cocoa tree density was approximately 600/ha. Further details on the climatic conditions, vegetation and ant arboreal fauna can be found in Leston (1978) and Delabie (1990). The soils of the plantation were podzols (Leite 1987), uniformly covered by 1 to 7 cm of dry litter. Litter biomass was estimated at 6.9 t/ha, lower than in commercial plantations of the same region (Leite 1987). All samples were taken in the litter or in the A soil horizon, which lies between 18 to 35 cm deep (Leite 1987) and contains the majority of cocoa tree roots (Cadima 1970). We denominate these roots as "superficial roots" because they are found immediately below the litter.

Soil samples

Within the 8 ha study area, 500 cocoa trees were individually numbered in a smaller 0.83 ha area. From June, 1986, until December, 1987, 51 weekly soil samples ($15 \times 15 \times 15$ cm), immediately below the litter layer, were taken 1.5 m from the trunk of each randomly chosen, numered, tree. The ants were immediately extracted by hand sorting. Samples were then sieved twice to recover ants not detected during the initial hand sorting. The ants were conserved in 70% alcohol and later identified in the laboratory. The 51 samples were treated independently, and species presence was registered. A percentage of 100% would mean that all of the 51 weekly samples held at least one individual of the species in question.

Litter samples

The litter samples were irregularly collected from February, 1987, to October, 1988, in the same experimental area, using the same spatial patterning. For each sample, 1 m^2 of litter near the trunk of a numbered tree was collected and its depth measured. The samples were extracted in a Berlese funnel for 48 hours, and then conserved in 70% alcohol and identified as in the case of the soil samples.

Data analysis

After identification, using the Kempf's (1972) nomenclature, the ant fauna of the litter was compared to that of the soil by a proportion test (Z) to characterize those species which could be considered as typical of each stratum. To estimate the total number of species of ants in the habitat which would be taken under our sampling conditions, we used the method of sequential progressive sampling (Lauga & Joachim 1987):

$$\mathbf{S = \frac{apr \cdot s \cdot (p - 1)}{(apr \cdot p) - s}}$$

where **apr** = "average point richness" (average number of species by sample); **s** = total number of species found in the samples; **p** = rank number of the last sample.

Results

A total of 124 ant species were recorded during our studies(Table 1). In 4,131 soil samples, of which 2,020 contained ants, we found 113 species, 55 being restricted to this stratum (Table 1). Similarly, in 525 litter samples, of which 427 contained ants, we registered 69 species, 11 of which were only sampled in this stratum (Table 1). Of those species present in both litter and soil samples, 17 had higher occurrence rates in litter, 10 in soil, and 31 had no significant differences in occurrence between soil and litter samples (Table 1). However, rank importance varied significantly between the two sampled strata (Table 1). In the litter stratum, *Solenopsis geminata medusae*, *Solenopsis* sp. 2 and *Wasmannia*

Table 1. The percentage of soil and litter samples in which each species was found, and the respective Z statistic. Also given is the descending rank of the species in the samples, with tied species sharing the same rank

Species	Percentage of all ants		
	Litter (Rank)	Soil (Rank)	Z
Ponerinae			
not identified	–	0.05	–
Amblyopone armigera Mayr	–	0.25 (52)	–
Anochetus mayri Emery	0.94 (32)	1.98 (14)	-1.86^{ns}
Anochetus sp. 1	0.70 (34)	0.05 (85)	1.60^{ns}
Belonopelta minima	0.23 (48)	0.15 (67)	0.34^{ns}
Ectatomma cf. *lugens* Emery	–	0.30 (47)	–
Gnaptogenys haenschi emery	–	0.20 (59)	–
Gnaptogenys minuta (Emery)	–	0.35 (44)	–
Gnaptogenys sp. 1	–	0.79 (27)	–
Gnaptogenys sp. 2	–	0.05 (85)	–
Gnaptogenys cf. *striatula* Mayr	–	0.05 (85)	–
Gnaptogenys cf. *horni* Santschi	–	0.15 (67)	–
Gnaptogenys striatula Mayr	4.22 (13)	0.13 (47)	4.00*
Hypoponera sp. 1	1.87 (23)	4.41 (06)	−3.17*
Hypoponera sp. 2	9.13 (06)	4.41 (06)	3.22*
Hypoponera sp. 3	–	0.25 (52)	–
Hypoponera sp. 4	–	0.05 (85)	–
Leptogenys crudelis (F. Smith)	–	0.45 (40)	–
Leptogenys pusilla Emery	–	0.10 (77)	–
Odontomachus haematodus (L.)	6.32 (08)	0.50 (38)	4.91*
Odontomachus minutus Emery	9.60 (05)	–	–
Pachycondyla apicalis (Latreille)	0.23 (48)	–	–
Pachycondyla constricta (Mayr)	–	0.05 (85)	–
Pachycondyla harpax (Fabr.)	1.64 (25)	1.83 (15)	-0.28^{ns}
Pachycondyla impressa Roger	–	0.20 (59)	–
Pachycondyla venusta (Forel)	–	0.54 (36)	–
Pachycondyla villosa (Fabr.)	0.23 (48)	0.15 (67)	0.34^{ns}
Pachycondyla sp. 1	0.47 (39)	2.52 (11)	−4.28*
Pachycondyla sp. 2	–	0.05 (85)	–
Pachycondyla sp. 3	0.70 (34)	–	–
Pachycondyla sp. 4	–	0.33 (44)	–
Proceratium brasiliense Borgmeier	–	0.20 (59)	–
Sphinctomyrmex stali Mayr	–	0.59 (34)	–
Thaumatomyrmex sp. 1	–	0.15 (67)	–
Typhlomyrmex pusillus Emery	0.23 (48)	0.20 (59)	0.14^{ns}
Typhlomyrmex sp. 1	–	1.58 (17)	–
Pseudomyrmecinae			
Pseudomyrmex flavidulus (F. Smith)	–	0.10 (77)	–
Pseudomyrmex cf. *gracilis* (Fabr.)	0.23 (48)	–	–
Pseudomyrmex gracilis (Fabr.)	–	0.05 (85)	–
Ecitoninae			
Eciton burchelli (Westwood)	0.23 (48)	–	–
Eciton vagans (Oliver)	–	0.05 (85)	–
Labidus coecus (Latreille)	0.47 (39)	4.46 (05)	−7.05*
Labidus praedator (F. Smith)	–	0.05 (85)	–
Nomamyrmex esenbecki (Westwood)	–	0.10 (77)	–

Table 1. (continued)

Species	Percentage of all ants		
	Litter (Rank)	Soil (Rank)	Z
Dolichoderinae			
Azteca bicolor Emery	–	0.05 (85)	–
Azteca sp. 1	–	0.10 (77)	–
Azteca sp. gr. *chartifex* Forel	–	0.20 (59)	–
Dolichoderus attelaboides (Fabr.)	–	0.05 (85)	–
Dolichoderus sp. 1	–	0.30 (47)	–
Linepithema humile (Mayr)	0.70 (34)	0.64 (31)	0.13^{ns}
Linepithema cf. *humile* (Mayr)	–	0.20 (59)	–
Linepithema sp. 1	–	0.05 (85)	–
Formicinae			
Acropyga decedens (Mayr)	0.23 (39)	3.56 (08)	– 7.02*
Acropyga cf. *paramaribensis* Borgmeier	1.41 (27)	58.07 (01)	–45.80*
Brachymyrmex sp. 1	0.47 (39)	0.35 (44)	0.34^{ns}
Camponotus cingulatus Mayr	4.22 (13)	0.69 (29)	3.56*
Camponotus sp. 1	–	0.15 (67)	–
Camponotus sp. 2	–	0.05 (85)	–
Nylanderia sp. 1	–	0.10 (77)	–
Paratrechina sp. 1	2.34 (19)	0.25 (52)	2.83*
Paratrechina sp. 2	4.45 (11)	0.20 (59)	4.24*
Paratrechina sp. 3	8.90 (07)	0.59 (34)	5.98*
Myrmicinae			
Attini			
Apterostigma sp. 1	0.47 (39)	0.30 (47)	0.49^{ns}
Cyphomyrmex rimosus (Spinola)	0.70 (34)	0.89 (26)	– 0.41^{ns}
Cyphomyrmex sp. 1	–	0.05 (85)	–
Mycocepurus goeldi Forel	2.34 (19)	0.54 (36)	2.40*
Myrmicocrypta sp. 1	0.23 (48)	1.09 (20)	– 2.60*
Sericomyrmex sp. 1	3.75 (15)	6.83 (03)	– 2.86*
Sericomyrmex sp. 2	1.41 (27)	5.15 (04)	4.97*
Trachymyrmex sp. 1	0.23 (48)	0.74 (28)	– 1.68^{ns}
Trachymyrmex sp. 2	0.23 (48)	0.69 (29)	– 1.54^{ns}
Solenopsidini			
Carebarella sp. 1	10.07 (03)	2.67 (10)	4.93*
Megalomyrmex symmetochus Wheeler	–	0.05 (85)	–
Monomorium floricola (Jerdon)	–	0.15 (67)	–
Monomorium sp. 1	0.23 (48)	0.05 (85)	0.77^{ns}
Oligomyrmex sp. 1	0.23 (48)	0.05 (85)	0.55^{ns}
Solenopsis brasiliana Santschi	0.23 (48)	–	–
solenopsis geminata (Fabr.)	–	2.82 (09)	–
Solenopsis geminata medusa Mann	44.03 (01)	1.63 (17)	17.53*
Solenopsis sp. 1	2.81 (16)	1.39 (19)	1.69^{ns}
Solenopsis sp. 2	13.82 (02)	1.09 (20)	7.55*
Solenopsis sp. 3	–	0.05 (85)	–
Tranopelta sp. 1	1.17 (30)	13.17 (02)	–13.10*
Myrmicini (Pheidolini)			
Pheidole sp. 1	4.92 (10)	1.53 (18)	3.13*
Pheidole sp. 2	1.64 (25)	0.45 (40)	1.89^{ns}
Pheidole sp. 3	1.17 (30)	1.09 (20)	0.14^{ns}
Pheidole sp. 4	1.87 (23)	0.64 (31)	1.81^{ns}

Table 1 (continued)

Species	Percentage of all ants		
	Litter (Rank)	Soil (Rank)	Z
Pheidole sp. 5	2.58 (18)	2.03 (13)	0.66^{ns}
Pheidole sp. 6	2.81 (16)	2.28 (12)	0.62^{ns}
Pheidole sp. 7	2.11 (21)	0.45 (40)	2.34*
Pheidole sp. 8	0.94 (32)	0.99 (25)	-0.10^{ns}
Pheidole sp. 9	0.23 (48)	0.20 (59)	0.14^{ns}
Pheidole sp. 10	2.11 (21)	0.25 (52)	2.64*
Pheidole sp. 11	0.23 (48)	–	–
Pheidole sp. 12	–	1.09 (20)	–
Pheidole sp. 13	–	0.10 (77)	–
Pheidole sp. 14	–	0.15 (67)	–
Pheidole sp. 15	1.17 (30)	0.05 (85)	2.14*
Pheidole sp. 16	0.23 (48)	0.05 (85)	0.77^{ns}
Pheidole sp. 17	–	0.45 (40)	–
Pheidole sp. 18	–	0.10 (77)	–
Pheidole sp. 19	0.47 (39)	–	–
Pheidole sp. 20	0.47 (39)	0.23 (58)	0.63^{ns}
Pheidole sp. 21	–	0.05 (85)	–
Other tribes			
Acantognathus sp. 1	0.47 (39)	0.05 (85)	1.25^{ns}
Adelomyrmex sp. 1	0.23 (48)	0.05 (85)	0.77^{ns}
Cephalotes atratus (L.)	0.23 (48)	0.15 (67)	0.34^{ns}
Crematogaster evallans Forel	–	0.05 (85)	–
Crematogaster cf. *limata* F. Smith	0.23 (48)	0.25 (52)	-0.05^{ns}
Crematogaster sp. 1	–	0.15 (67)	–
Crematogaster sp. 2	–	0.25 (52)	–
Dacetini not identified	0.23 (48)	–	–
Gymnomyrmex rugithorax Kempf	0.70 (34)	0.05 (85)	1.60^{ns}
Octostruma jheringhi (Emery)	0.47 (39)	1.68 (16)	−2.78*
Octostruma stenognatha Brown/Kempf	5.85 (09)	0.15 (67)	5.01*
Rogeria sp. 1	–	0.30 (47)	–
Rogeria sp. 2	0.23 (48)	0.10 (77)	0.55^{ns}
Rogeria sp. 3	1.41 (27)	0.50 (38)	1.54^{ns}
Rogeria sp. 4	–	0.05 (85)	–
Rogeria sp. 5	–	0.64 (31)	–
Stegomyrmex sp. 1	–	0.05 (85)	–
Strumigenys sp. 1	4.45 (11)	–	–
Tetramorium sp. 1	0.47 (39)	–	–
Wasmannia auropunctata (Roger)	10.07 (03)	1.09 (20)	6.09*

auropunctata were dominant, with the former being more than 30% mor common than the second ranked species (Table 1). For the soil stratum *Acropyga* cf. *paramaribensis* was by far the dominant ant, followed by *Tranopelta* sp. 1 (Table 1).

The collector's cumulative curves for litter and soil strata (Fig. 1) were used to estimate total species richness for the soil and litter strata. Our average point richness (**apr**) for litter was 1.54, and for soil, 0.74. Using these parameters we estimated litter species richness (**S**) at 75.3, and soil species richness at 117.3.

By interpolation of the collector's curves, we estimated that the number of samples necessary to obtain half of the number of species in each stratum were 75 for litter and 500 for soil. This estimate depends upon the methods used to collect the ants and the heterogeneity of

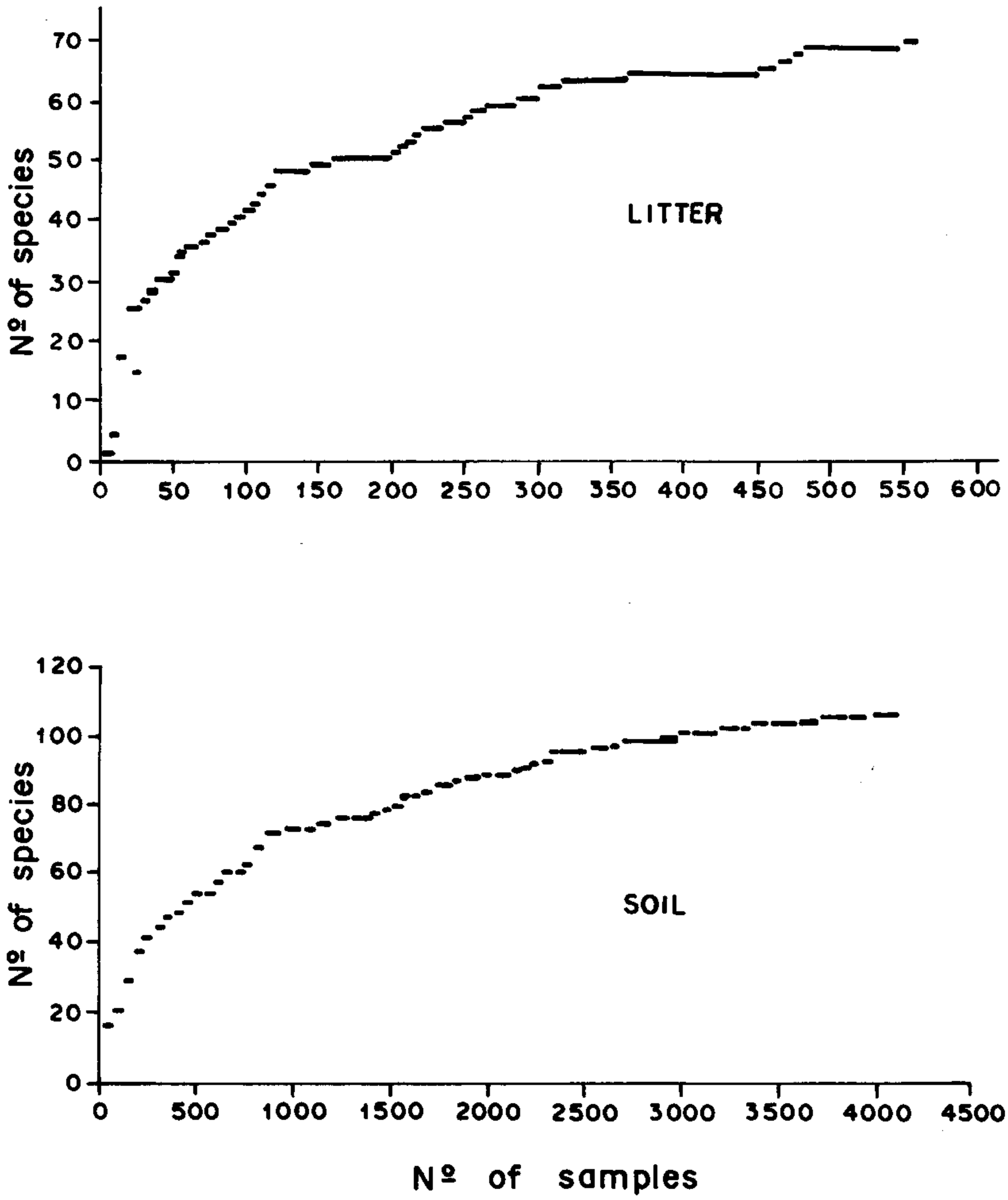

Fig. 1. Collector's curve for ant species in the two studied systems

the ant populations. In this case, the Berlese funnel sampling of litter was evidently more efficient than hand sampling of soil for extracting the ants. Even in this case, for two populations expected interdependent, the efficency of sampling would have to be compared by the values of the respective **apr**. Thus, twice as many samples of litter would be necessary to collect half the number os soil ants. If this relation does not hold, we would have to conclude that the soil ant fauna was particularly heterogeneous, dispersed, or very rich with a high number of rare species in concordance with the dispersion hypothesis, when compared with the litter fauna which was more homogeneous, and characterized by high species density.

The ant species rank-abundance curves for the two sampled strata fit a regular log-normal distribution (Fig. 2). Both assemblages demonstrate a similar structure with two dominant species each, and with a very high number of rare species, principally in the soil.

0 to 7 ant species were recorded per Berlese sample, with litter depth varying from 0.5 to 7.0 cm (Fig. 3). One ant species was generally found in 1 m^2 of 2 cm deep litter, with the richest samples found in the 1.5 to 2.5 cm thickness class. However, when the percent species frequencies were plotted against litter thickness, grouped in five classes (Fig. 4), no statistical differences were detected between classes, indicating that litter thickness did not significantly influence the local faunal richness.

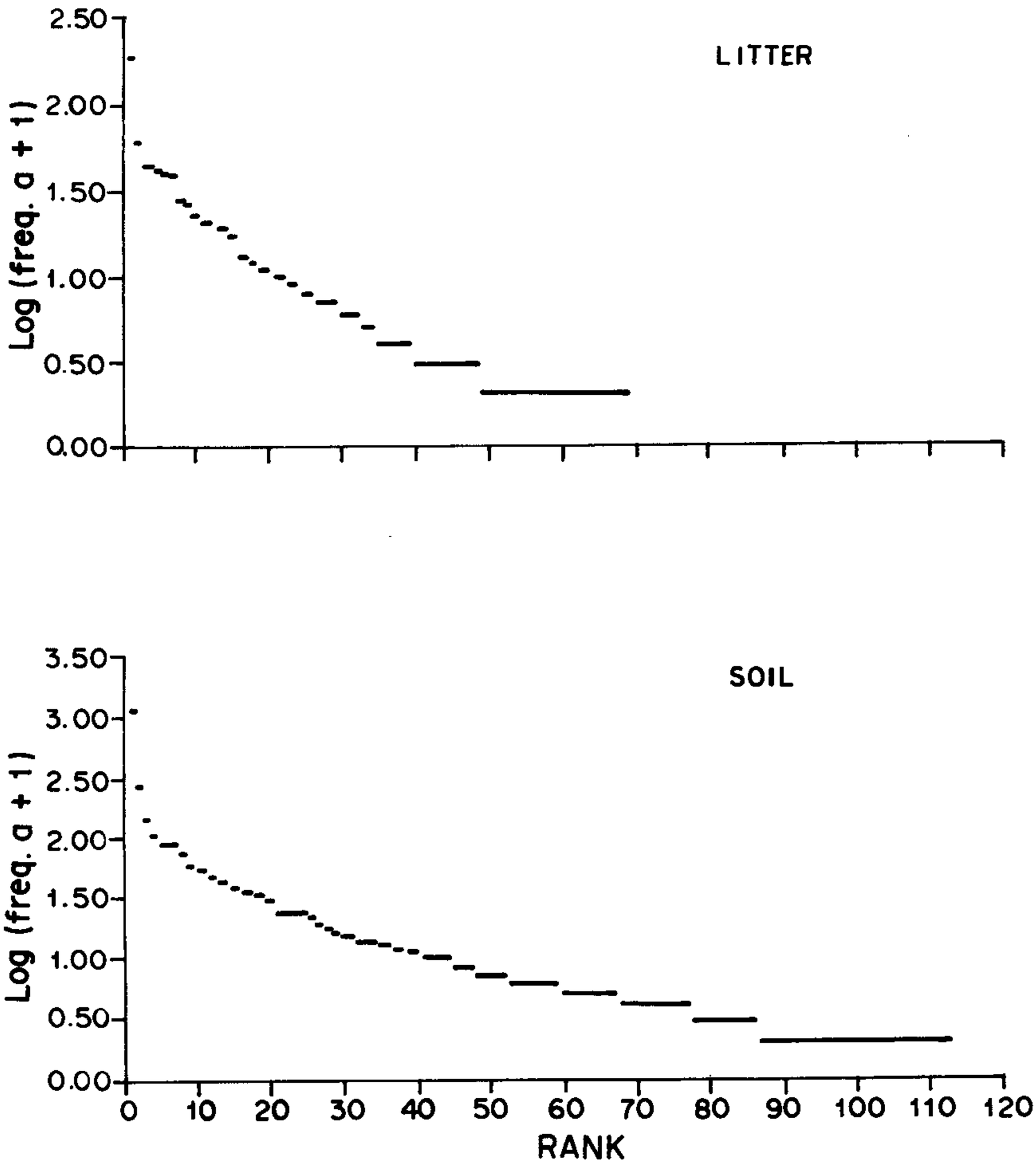

Fig. 2. Species rank-abundance relations for the ant species in the two systems studied

Discussion

In spite of the high species richness, characteristic of tropical environments, we found a strong numerical species dominance in both of the studied assemblages. Dominant species are characteristic of ground, and other strata, of tropical ant faunas (Fowler et al. 1991). Furthermore, collector's curves for both strata indicated that we had obtained a fair characterization of the ant fauna of each. Although the litter stratum had half as many species as the subterranean stratum (69 vs 113), 58 species were common to both strata.

Ground ant communities are assumed to be organized around food resources and nesting sites (Culver 1974). The epigaeic, litter, ant fauna consists of generalized, opportunistic feeders (Fowler et al. 1991). Higher species richness in the subterranean hypogaeic fauna is probably due to the fact that subterranean ants are generally more specialized that the epigaeic species. The cryptic ants *(sensu lato)* belong to highly specialized groups which probably can not compete with ecologically plastic genera such as *Pheidole*, established in the same stratum. In the case of specialized cryptic ant predators, colony populations should be low. This is because a high degree of specialization will almost always correspond to prey resource limitation. However, for cryptic ant non-predators, such as *Acroyga*, a colony

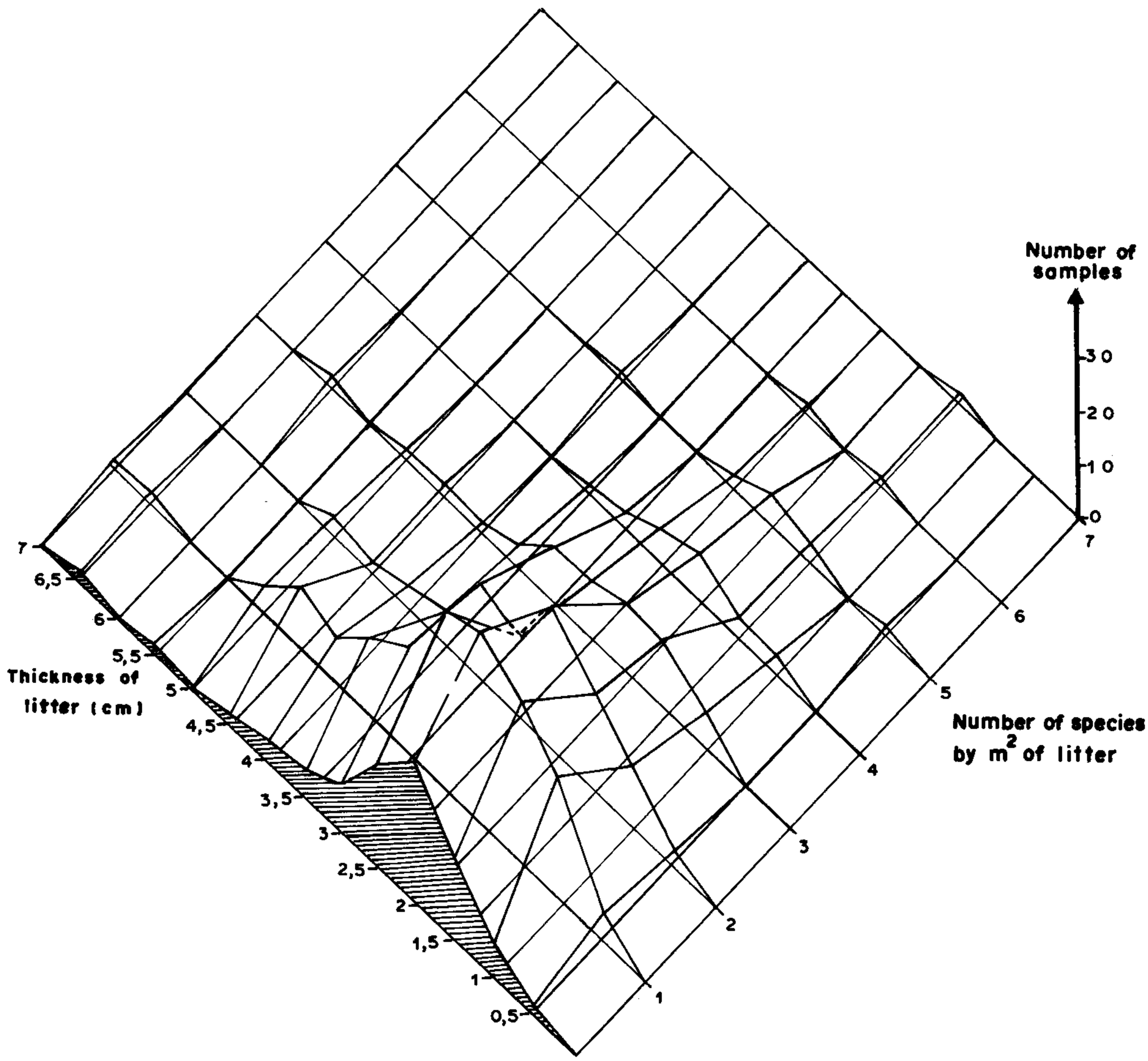

Fig. 3. Frequency distribution of ant species richness by litter depth

may contain several hundred to thousands of individuals. Large colony populations in these cases probably result from the ants' abilities to regulate that food resource population. The cryptic nature may have selected for the development of very original reproductive strategies, such as found in queens of *Acropyga*, which fly away with a reproductive stage of its symbiotic mealybug during the nuptial flight, a process analogous to that of Attine queens which carry pieces of mycelium of its symbiotic fungi during mating flights (Flanders 1957; Delabie 1990).

Many ground nesting species explore superficial vegetation, like the Attini which use fragments of leaves or flowers to cultivate their symbiotic fungus, or *Pheidole* which may use seed fragments in its diet. Some generalist litter species, such as *W. auropunctata*, facultatively use vegetation to rear Homoptera for honeydew used to feed larvae and to expand the colony. Other species, like *Ectatomma tuberculatum*, nest in the soil and are territorial in one tree directly associated with the nest. Furthermore, Greenslade & Greenslade (1977) note that epigaeic species "exclude even dominant arboreal ants from the ground layers". Arboreal ants are generally more specialized that epigaeic species (Fowler et al. 1991).

The nature of the vegetation will determine the existence and the importance of the litter layer. Litter thickness, which depends on various factors such as sunlight, rain impact, and nutrient and water absorption capacity, may influence food resource availability, but was

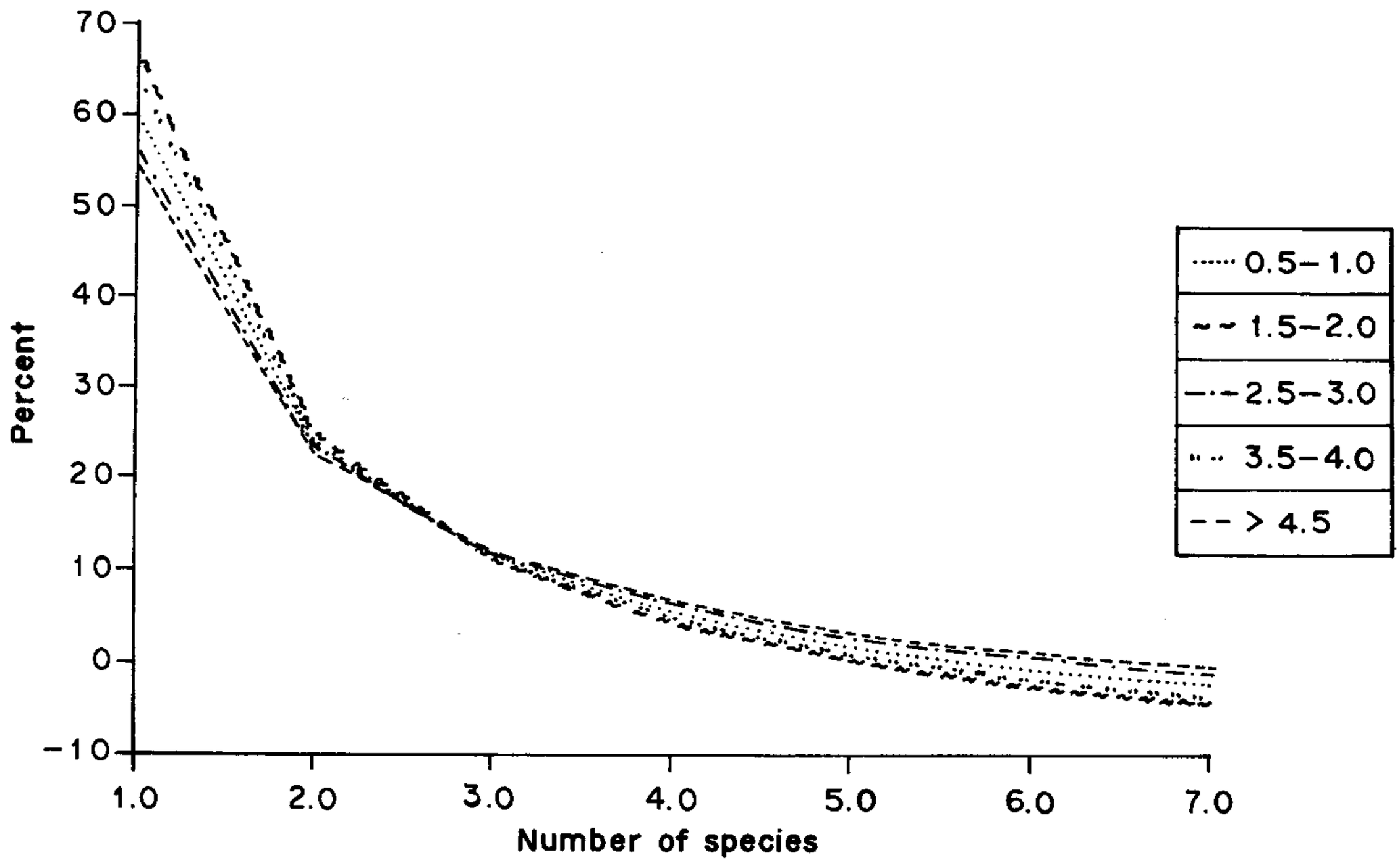

Fig. 4. The percent distribution of ant species richness per litter depth class. Curves are not significantly different

not found to affect local ant fauna richness. This was probably due to the relatively high colony mobility and the patchy distribution of most tropical ant species (Levings 1983). However, Levings & Windsor (1984) found positive correlations between litter moisture and the abundance of some groups of soil arthropods, auch as Formicidae, Coleoptera, Collembola, Homoptera, Isopoda and Diplopoda in a tropical seasonal deciduous forest. In our study area, humidity is always high and rains are frequent. Litter is thus always moist. Moisture probably influences numbers by increasing rates of decomposition and fungal growth, which is the food base of a great part of litter arthropods. In consequence, predatory ants may be favoured by high litter moisture, because of increased prey availability (Levings 1983; Levings & Windsor 1984).

The litter is where the organic matter is mineralized and where a rich and specific fauna and microflora are active. In tropical regions, the main litter arthropods are the Insecta (Blattaria, Gryllidae, Thysanura, Psocoptera, Hemiptera, Homoptera, Coleoptera, Formicidae, Diplura, Collembola, Isoptera, larvae of Diptera and Lepidoptera), Araneidae (Opilionides, Pseudoscorpionida, Aranea and Acarina), Amphipoda, Isopoda, Chilopoda, and Diploploda (Lavelle & Kohlmann 1984; Levings & Windsor 1984). The abundance of potential prey sustains an abundance of generalist and specialist predators.

In tropical soils, the rhizosphere is an important trophic level for the soil fauna. The superficial root system of the cocoa trees forms a 15–20 cm thick layer, immediately below the litter, which "acts as a filter, resorbing all the nutrients released by litter decomposition" (Lavelle 1984). Few genera of ants are able to rear subterranean mealybugs, as can *Acropyga*, and apparently, *Tranopelta*, in South America (Bunzil 1935). Ecologically, the rhizosphere is an excellent place to establish an ant colony under tropical conditions. It provides brood and adults with an almost infinite availability of food, if the ant depends on honeydew or even vegetable matter. Furthermore, it provides favorable humid and warm nest conditions, reducing the energetic costs of internal activity of the society. The major problems for rhizosphere ants are the numerous predators which may occur in the same space. This contigency may be met, for example, in the case of *Acropyga*, by the construction of a

network inter-connected galleries to form a relatively closed nest site. But, why does a specialized "root-cutting" Attine not exist there?
The predatory ants are either omnivorous, facultative hunters, generalist predators, such as the large Ponerinae, or specialized predators, like the rarest soil Ponerinae, which we consider to be the true cryptic species of this group. Surprisingly, data do not exist on specialist predators of such common subterranean organisms as the soil mites in South America. Although our survey has indicated strong patterns of dominance and a high species richness in tropical forest litter and subterranean soil ant assemblages. Many species are found in both strata, and may indicate large niche breadths. The species rich subterranean fauna is characterized by many dietary specialists, but we are not at present able to characterize ecologically all of the species encountered in the soil samples, and further studies are necessary to understand their role in tropical forest ecosystems.

Acknowledgements

Studies were supported by the Conselho Nacional de Desenvolvimento Cientifico e Teconologico (CNPq) of Brazil, through grants to both authors. Supplementary support was provided by CEPLAC and UNESP. We thank Maria Thereza Fink for her constant love, encouragement and support, and Ana Maria Dias de Aguiar and Marcos Antonio Pesquero and an anynomous reviewer for their comments on earlier versions of this paper.

References

Andersen, A. N. (1987) Ant community organization and environmental assessment. In: Majer, J. D. (ed) The role of invertebrates in conservation and biological survey. Western Australia Department of Conservation and Land Management Report, Perth.

Borgmeier, T. (1927) Um caso de trophobiose entre uma formiga e um parasita do caféeiro. Bol. Mus. Nac. Rio de Janeiro **3**, 285–289.

Bunzli, G. H. (1935) Untersuchungen über coccidophile Ameisen aus den Kaffeefeldern von Surinam. Mitt. Schweiz. Entomol. Gesell. **16**, 455–593.

Cadima, A. (1970) Estudo do sistema radicular do cacaueiro em alguns tipos de solos da região cacaueira do Sul da Bahia. Bol. Téc. **5**, CEPLAC, Itabuna, Bahia (Brazil), 31 pp.

Culver, D. C. (1974) Species packing in Carribbean and North temperate ant communities. Ecology **55**, 974–988.

Delabie, J. H. C. (1990) The ant problems of cocoa farms in Brazil. In: Vander Meer, R. K., Jaffe, K. & Cedeno, A. (eds) Applied myrmecology: a world perspective. Westview Press, Boulder.

Delabie, J. H. C., Mantovani, J. E., Mauricio, I. (1991) Observações sobre a biologia de duas espécies de *Acropyga* (Formicidae, Formicinae, Plagiolepidini) associadas a rizosfera do cacaueiro. Rev. Brazil. Biol. **51**, 185–192.

Flanders, S. E. (1957) The complete interdependence of an ant and a coccid. Ecology **38**, 535–536.

Fowler, H. G., Forti, L. C., Brandão, C. R. F., Delabie, J. H. C., Vasconcelos, H. L. (1991) Ecologia nutricional de formigas. In: Panizzi, A. R. & Parra, J. R. P. (eds) Ecologia nutricional de insetos e suas implicações no manejo de pragas. Editora Manole, São Paulo.

Greenslade, P. J. M., Greenslade, P. (1977) Some effects of vegetation cover and disturbance on a tropical ant fauna. Ins. Soc. **24**, 163–182.

Kempf, W. W. (1961) A survey of the ants of the soil fauna in Surinam (Hymenoptera: Formicidae). Studia Ent. **4**, 481–524.

Kempf, W. W. (1972) Catálogo abreviado das formigas da região Neotropical (Hymenoptera: Formicidae). Studia Ent. **15**, 3–344.

Lauga, J., Joachim, J. (1987) L'echantillonnage des populations d'oiseaux par la méthode des E. F. P.: intérêt d'une étude mathématique de la courbe de richness cumulée. Oecol. Gener. **8**, 117–124.

Lavelle, P. 1894) The soil system in the Humid Tropics. Biol. Intl. **9**, 2–17.

Lavelle, P., Kohlmann, B. (1984) Etude quantitative de la macrofaune du sol dans une forét tropicale humide du Mexique (Bonampak, chiapas). Pedobiol. **27**, 377–393.

Leite, J. de O. (1987) Caractéristicas do manto detritico e sua relação com a fertilidade da camada superficial do solo en plantações de cacua. Bras. Cienc. Solo **11**, 45–49.
Leston, D. (1978) A Neotropical ant mosaic. Ann. Entomol. Soc. Am. **71**, 649–653.
Levings, S. C. (1983) Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. Ecol. Monogr. **53**, 435–455.
Levings, S. C., Franks, N. R. (1982) Patterns of nest dispersion in a tropical ground ant community. Ecology **63**, 338–344.
Levings, S. C., Windsor, D. M. (1984) Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. Biotropica **16**, 125–131.
Petal, J. 1978) The role of ants in ecosystems. In: Brian, M. V. (ed) Production ecology of ants and termites. Cambridge University Press, Cambridge.
Roba, R. P. (1936) Un nouveau coccide signalé sur caféier. Bull. Ann. Soc. Ent. Belg. **76**, 297–298.
Strickland, A. H. (1945) A survey of the arthropod soil and litter fauna of some forest reserves and cacao estates in Trinidad, British West Indies. J. Anim. Ecol. **14**, 1–11.
Weber, N. A. (1944) The Neotropical coccid-tending ants of the genus *Acropyga* Roger. Ann. Entomol. Soc. Am. **37**, 89–122.
Wilson, E. O. (1959) Some ecological characteristics of ants in New Guinea rain forests. Ecology **40**, 437–447.