Spatial and Temporal Variation in the Abundance and Diversity of Ants (Hymenoptera: Formicidae) in the Soil and Litter Layers of a Maryland Forest

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ABSTRACT: Spatial and seasonal variation in the abundance and community composition of terrestrial ants was studied in a mature deciduous forest located on the inner coastal plain of Maryland. Monthly samples of soil and litter during the March-October activity season yielded a total of 22 ant species, but the 10 most abundant species accounted for more than 95% of the individuals collected. The single most abundant ant species in the soil layer (*Brachymyrmex depilis*) was rare in the litter layer, but there were few other major qualitative differences in the species inhabiting the two vertical strata. However, the density of ants per unit of surface area was more than three times as high in the upper 10 cm of soil as in the overlying litter. Marked seasonal differences in ant abundance and community composition were significantly correlated with surface temperature, but were largely independent of substrate moisture content and standing crop of leaf litter. The observed patchiness in the horizontal distribution of ants was unrelated to position along the modest local topographic gradient. The high values measured for ant density (mean monthly density = 816 m^{-2}) and biomass (mean monthly dry mass = 144 mg m^{-2}) strengthen previous suggestions that ants constitute a significant component of the macroarthropod fauna in temperate forest ecosystems.

INTRODUCTION

Although it is generally accepted that ants (Hymenoptera: Formicidae) are abundant in forested ecosystems (*e.g.*, Wilson, 1971, 1987; Fittkau and Klinge, 1975; Baroni-Urbani and Pisarski, 1978; Petal, 1978; Petersen, 1982b; Levings, 1983), there are surprisingly few published quantitative studies of temperate-zone forest ant communities. Surveys in the central USA (Headley, 1943, 1949, 1952; Talbot, 1957, 1965, 1975) and in southern Canada (Letendre *et al.*, 1971; Letendre and Pilon, 1972; Francoeur, 1965, 1966) have revealed extraordinarily high densities of individual worker ants and ant colonies in North American forests, but the cited studies did not consider seasonal and microgeographic variation. In two earlier studies conducted in Maryland (Lynch *et al.*, 1980; Lynch, 1981), we quantified seasonal, successional and vertical niche partitioning among the ants in a temperate forest, but we assessed only the litter and low arboreal strata. The present study was designed to determine if the soil layer, which had been ignored in our previous surveys, constitutes a distinctive and quantitatively important vertical stratum in the same community. The specific goals of this study were (1) to describe the species composition and determine the absolute density of soil-dwelling ants; (2) to quantify similarities and differences between soil- and litter-inhabiting components of the ant community, and (3) to assess the responses of ants in both vertical strata to seasonal and microgeographic variation in their environment.

STUDY SITE

Research was conducted in 1980 and 1981 at the Smithsonian Institution's Environ-

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mental Research Center, a 1000-ha ecological reserve located on the inner coastal plain
of Maryland, approximately 10 km SW of Annapolis, Anne Arundel Co. The study
site was located within a 40-ha tract of mature broadleaf deciduous forest which was
designated by Brush *et al.* (1980) as part of the widespread tulip poplar association. The
forest canopy averaged 20-30 m in height, and was dominated by tulip poplar (*Liriodendron tulipifera* L.), American beech (*Fagus grandifolia* Ehr.), hickories (*Carya glabra* Miller
and *C. tomentosa* Poiret), sweetgum (*Liquidambar styraciflua* L.) and oaks (*Quercus alba* L.,
Q. velutina Lambert and *Q. falcata* Michaux). The floristic composition of this forest,
which has not been clear-cut in more than a century, is described in more detail by
Lynch (1981). Ants were sampled within a 2-ha (400 m x 50 m) section of forest that
encompassed a 12-m elevational gradient from the top of a knoll to the bank of North
Branch, a small intermittent stream. The vegetation and the subdued rolling topography of the study site are typical of forested sections of mid-Atlantic inner coastal plain.

METHOD

Field work was conducted in two parts. In 1980 a row of 20 contiguous 20 m x 20 m
quadrats was surveyed along an E-W axis extending from the top of the above-
mentioned knoll to the center of the floodplain of North Branch (Fig. 1). Using a metal
stake at the center of each plot as a reference point, we chose a different set of randomly
selected E-W and N-S coordinates on each sampling day. At the designated sampling
point, a 0.1-m² metal frame was pounded into the ground, and the leaf litter enclosed
by the frame was quickly scooped into a sealable plastic bag. A section of metal pipe
(diam = 15 cm) was then driven 10 cm into the soil at the center of the sampling
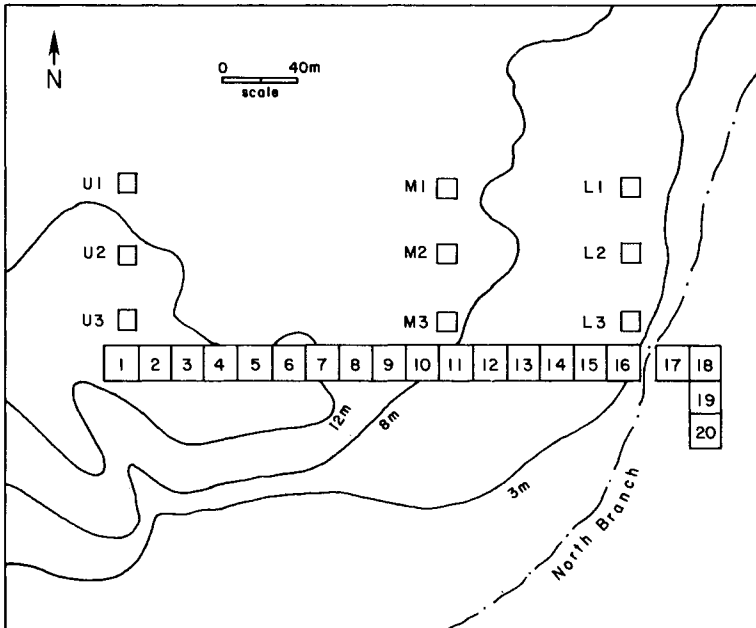

Fig. 1. — Map of study area showing sampling layout for 1980 (large numbered quadrats)
and 1981 (small quadrats). Areas below the 3-m contour (quadrats 17-20) were within the
floodplain of North Branch. The sampling areas used in 1980 were 20 m x 20 m; those used in
1981 were 5 m X 5 m, and were arranged in triplets at the upper (U1, U2, U3), middle (M1,
M2, M3), and lower (L1, L2, L3) portions of the E-facing slope

frame. The resulting soil core was removed from the pipe, broken into pieces, and sealed in a second plastic bag. At each of the 20 sampling stations we measured temperature 1.5 m above the substrate, just beneath the surface of the litter and at a depth of 10 cm in the soil. Available soil moisture (expressed as centibars of soil suction) was measured at a depth of 10 cm using a Quick Draw brand portable tensiometer.

Monthly samples of litter and soil were collected between March and October 1980, yielding a total of 160 soil samples and 160 litter samples. Ants were extracted using an array of 40 large Berlese funnels (diam = 0.5 m), each equipped with a 60-w incandescent bulb mounted 60 cm from the material being processed. Soil samples were coarsely crumbled before being put into the funnels in order to help promote even drying of the soil. Escape of ants was prevented by coating the inner surfaces of the metal funnels with talcum powder. Samples were processed for 7 days, by which time no additional ants or other arthropods were observed to appear in collecting jars that were attached to the funnels. Preliminary experimental runs using known numbers of ants indicated an extraction efficiency rate of more than 85% for both litter and crumbled soil. Extraction efficiency was considerably less for intact soil cores.

Litter samples were weighed at the time of collection and after 1 week of drying in the Berlese funnels, and the difference between the two mass determinations was used to compute the percent available moisture in the litter. Accurate gravimetric determination of soil moisture was not possible due to the loss of soil particles into the alcohol-filled collecting jars. In any event, available soil moisture (*i.e.*, soil suction, as measured with the tensiometer) probably is more relevant than gravimetric water content to ants and other small soil-inhabiting animals.

The second part of the study took place in August and September 1981, when we conducted an intensive short-term sampling program aimed at quantifying the spatial components of patchiness in ant density within the litter layer. For this study we surveyed three parallel 5 m x 45 m quadrats at the upper, middle and lower portions of the 1980 transect site. Each quadrat contained three 5 m x 5 m sampling areas separated from one another by a 15-m buffer zone (Fig. 1). The long dimensions of the quadrats were perpendicular to the 1980 elevational transect, such that the three sampling areas within a given quadrat were all at the same elevation. On each of two sampling dates (17 August and 3 September) five sets of N-S and E-W coordinates were randomly selected within each of the nine sampling areas, and a 0.1-m² litter sample was collected at each designated point. The resulting 45 samples for each date were processed as described for the 1980 samples, and the resulting data on ant abundance and species occurrence were subjected to a model II nested ANOVA (Sokal and Rohlf, 1969). For this analysis the 5 m x 5 m sampling plots were nested within the three elevational blocks in order to distinguish the effects of topographic position (hilltop vs. midslope vs. lower slope) from those of large-scale horizontal patchiness (differences among 5 m x 5 m plots at a given elevation). The data also were subjected to stepwise linear multiple regression analysis (Draper and Smith, 1966) to examine the independent effects of litter mass and litter moisture as predictors of ant abundance and species richness on a given day.

RESULTS

The ant fauna.—The 1980 sampling program yielded a total of 4124 individual ants that represented 22 species (Table 1). Previous studies had shown that the local mosaic of successional and climax habitat types supports an ant fauna of ca. 60 species (Lynch, 1981), so the litter and soil layers of the small forested tract we sampled contained about one third of the species in the regional species pool. No additional ant species were revealed by the short-term sampling program of 1981, and the comments in this section pertain only to the 1980 data.

Seven of the 22 ant species collected in 1980 were represented by fewer than five individuals; from 5-1902 individuals of the remaining 15 species were collected (Table 1).

Dominance (*i.e.*, the relative abundance of the commonest species) was high for both the litter and the soil components of the ant community. The single most abundant species in the litter samples (*Paratrechina faisonensis*) accounted for 61.2% of the individuals collected, and the combined dominance of the three commonest species (*P. faisonensis, Ponera pennsylvanica* and *Smithistruma ohioensis*) was 79.8%. Ant numbers were somewhat more equably distributed among species in the soil samples, where the single most abundant species (*Brachymyrmex depilis*) accounted for only 38.1% of the total individuals, and the three commonest species (*B. depilis, Paratrechina faisonensis,* and *Ponera pennsylvanica*) together made up 69.5% of the total.

Seasonal and spatial variation in the microenvironment.—One goal of our study was to test the hypothesis that ant occurrence is systematically related to sample measurable prop-

TABLE 1.—Number of individuals (N) and frequency of occurrence (F) of ants in monthly soil cores and litter samples collected March-October 1980. D(1) is the proportion of the total individuals or occurrences contributed by the single most abundant (or frequent) species. D(3) is the proportional contribution of the three most abundant species. *See* text for details of sampling methods

Species	Soil Samples (n = 160)				Litter Samples (n = 160)			
	N	rank	F	rank	N	rank	F	rank
Ponerinae								
Amblyopone pallipes	2	(15)	2	(14)	3	(14)	3	(13)
Ponera pennsylvanica	160	(3)	38	(1)	228	(3)	32	(3)
Proceratium sp.	1	(17)	1	(16)	0	(21)	0	(21)
Myrmicinae								
Aphaenogaster fulva	0	(19)	0	(19)	14	(11)	4	(11)
A. rudis	132	(4)	25	(3)	62	(6)	40	(1)
Leptothorax curvispinosus	5	(13)	3	(12)	198	(4)	9	(8)
L. longispinosus	0	(19)	0	(19)	1	(18)	1	(17)
L. schaumi	0	(19)	0	(19)	1	(18)	1	(18)
Myrmecina americana	100	(5)	28	(2)	48	(7)	15	(5)
M. punctiventris	13	(9)	4	(10)	68	(5)	10	(7)
Smithistruma ohioensis	91	(6)	11	(7)	251	(2)	27	(4)
S. ornata	10	(10)	4	(10)	48	(7)	8	(9)
S. rostrata	0	(19)	0	(19)	2	(16)	1	(17)
Stenamma diecki	9	(12)	9	(8)	10	(12)	8	(9)
S. impar	16	(8)	15	(6)	16	(10)	13	(6)
Dolichoderinae								
Tapinoma sessile	0	(19)	0	(19)	1	(18)	1	(17)
Formicinae								
Brachymyrmex depilis	591	(1)	24	(4)	3	(14)	3	(13)
Camponotus impressus	2	(15)	2	(14)	0	(21)	0	(21)
Lasius alienus	10	(10)	6	(9)	40	(9)	4	(11)
L. umbratus	83	(7)	2	(14)	0	(21)	0	(21)
Paratrechina faisonensis[*]	327	(2)	18	(3)	1575	(1)	40	(1)
Prenolepis imparis	0	(19)	0	(19)	4	(13)	2	(15)
Totals	1551		220		2573		221	
Dominance								
D(1)	.381		.173		.612		.181	
D(3)	.695		.382		.798		.507	

[*] This species listed as *P. melanderi* in Lynch (1981) and Lynch *et al.* (1980). *See* Trager's (1984) taxonomic revision of *Paratrechina*.

erties of the physical environment, specifically substrate moisture, temperature, topo-
graphic position and litter mass (Lynch *et al.,* 1980; Lynch, 1981; Levings and Wind-
sor, 1984). Mean soil temperature at a depth of 10 cm increased from 5 C in March to
a maximum of 24 C in August, then declined to approximately 20 C in September and
October (Fig. 2B). Litter temperature in March averaged ca. 5 C higher than soil tem-
perature, but this differential had disappeared by midsummer; by July and August ants
within the top 10 cm of soil and the litter experienced essentially the same thermal envi-
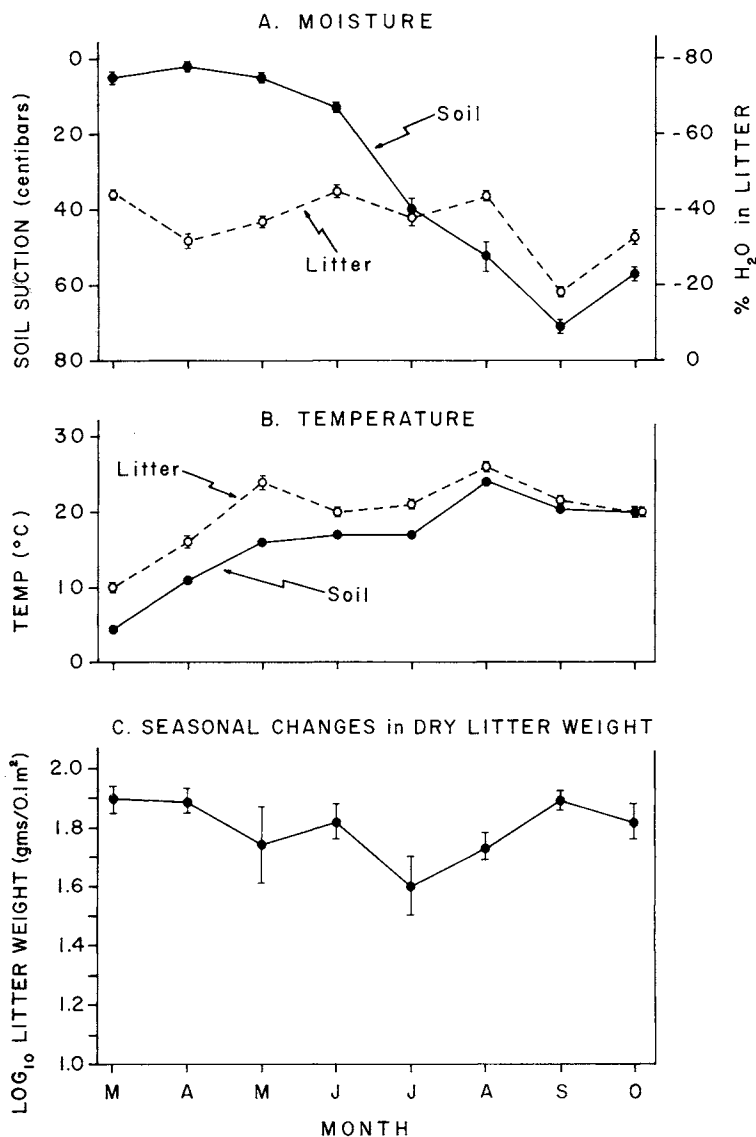ronments.

Fig. 2. — Summary of seasonal variation in soil and litter moisture, soil and litter tempera-
ture, and dry mass of leaf litter (± 1 SE). Where no error bars are indicated, the standard er-
ror of the mean was less than the diameter of the symbol

Mean moisture content of the leaf litter averaged ca. 42% of fresh litter mass in March; litter moisture content remained above 30% until September, when it declined to a seasonal low of ca. 25% (Fig. 2A). In contrast, available soil moisture declined steadily throughout summer and early autumn (Fig. 2A). These two patterns suggest that the combination of rainfall from summer showers and "wicking" of moisture from the underlying soil provided sufficient water to maintain fairly high moisture levels in the litter layer during 1980, despite the gradual drying of the soil that occurred over the summer. There was no consistent elevational pattern in soil moisture or litter moisture except within the floodplain of North Branch, where available soil moisture remained consistently high (soil suction 45 centibars) throughout the entire 8-month study period. Similarly, litter mass did not vary significantly with topographic position, except in the four floodplain quadrats, where the standing crop of litter in any given month was significantly ($P < .001$) lower than it was on the adjacent slope. There was substantial seasonal variation in the standing crop of litter, the seasonal minimum (400 g m²) occurring in July (Fig. 2C).

Seasonal trends in ant abundance and species richness. —Although the surface area sampled by the soil cores (.018 m²) was less than 20% that of the litter samples (0.1 m²), soil cores and litter samples contained similar numbers of individual ants and ant species in any given month (Fig. 3A, 3B). The maximum number of litter species (13) was found in June, but species richness in the litter samples was nearly as high in May, July and August. A similar broad seasonal peak in species richness was observed in the soil samples, but there the maximum (14 species) occurred in May rather than June, and a steep decline had occurred by August (Fig. 3B). Between April and September, the months when ant activity was sufficiently high to allow meaningful comparisons, the pooled species richness for soil and litter samples was only marginally higher than the larger of the two individual diversity values (Fig. 3B), a reflection of the fact that the ant species occurring in one layer tended to be a subset of those in the other.

Exp (H'), which can be interpreted as the effective number of equally abundant species, is a useful index to diversity if one wishes to reduce the effect of very rare species (Hill, 1973; Alatalo and Alatalo, 1977; Lynch, 1981). Exp (H') tended to vary in parallel with changes in simple species richness, but month-to-month variation in species number were damped, and distinctions between the two layers were reduced by expressing diversity in terms of equally abundant species (Fig. 3C). In both the soil and the litter samples, the number of equally abundant species increased from a minimum of 5-6 in March to a maximum of 10-11 in May (soil) or June (litter), then declined to 5-6 in October.

Relationship of physical factors to ant occurrence. —Multiple regression analysis of the eight monthly collections from 1980 revealed that temperature was the only consistent correlate of either the number of individual ants or the number of species occurrences in either the litter or the soil layer (Table 2). Of the other physical variables whose effects were tested, only litter mass contributed significantly to the prediction of ant abundance or the number of species occurrences. However, the sign of this correlation was negative, indicating that more ants occurred in samples with low litter mass.

The greater sampling intensity for late summer 1981 allowed us to analyze the effects of physical variables at one time of the year. Results of the nested ANOVAs of litter samples collected in August (n = 45) and September (n = 45) 1981 agreed with the 1980 study in showing no statistically significant effects of topographic position on the abundance or species richness of ants (Table 3). However, the 1981 collection did show highly significant ($P < .01$) variation in ant density among 5 m x 5 m plots at a given topographic position (Table 3). Thus, the abundance of litter ants was patchy at the scale of the 5 m x 5 m sampling plots, but patchiness was independent of position along the modest elevational gradient.

Litter moisture was more variable than litter temperature among sampling locations on both of the two 1981 sampling dates (coefficients of variation = 129 vs. 52 for Au-

gust; 106 vs. 30 for September). Separate stepwise regression analyses for the two sets of samples revealed that in both months microgeographic variation in litter moisture was significantly ($P < .01$) and positively correlated with total ant abundance. The commoner individual ant species (*e.g., Ponera pennsylvanica* and *Paratrechina faisonensis*) also tended toward high density at moister sites, although correlations for individual species fell short of statistical significance. One might have predicted, *a priori*, that areas with deep litter would retain more water than would areas with scant litter (*i.e.,* that litter mass per quadrat would be positively correlated with percent litter moisture), but no
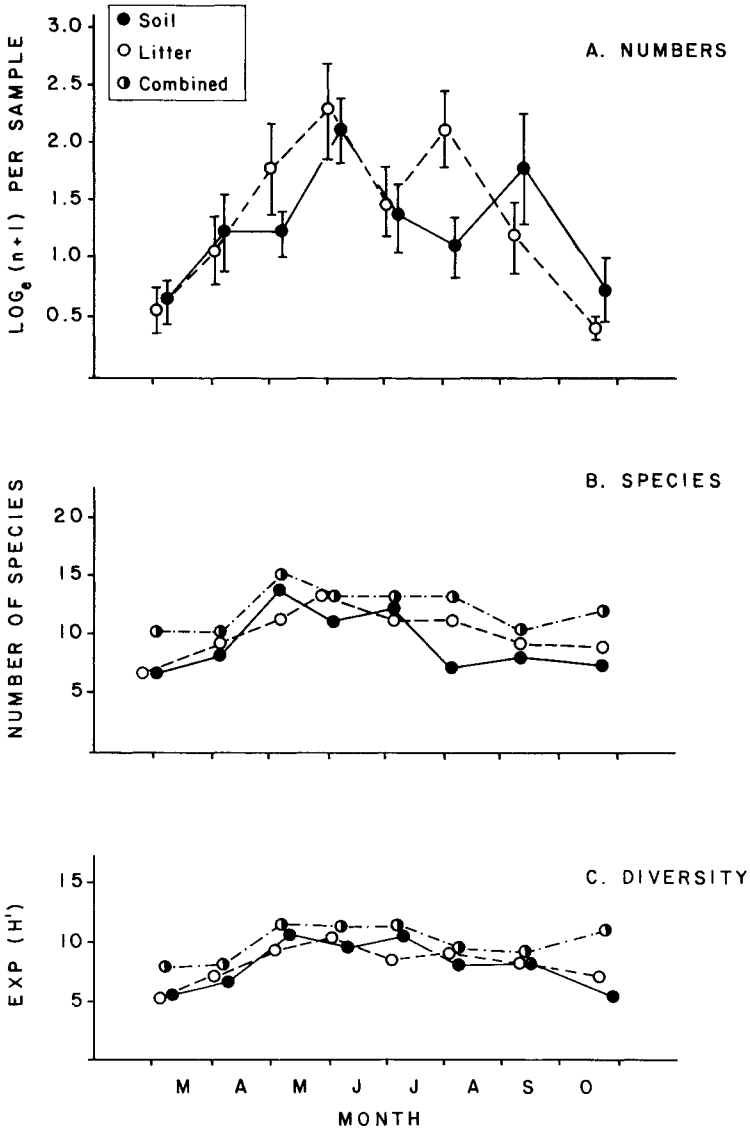

Fig. 3. — Summary of seasonal variation in abundance (± 1 SE), species richness and diversity [exp (H')] of ants in the soil and litter samples

such correlation was found (for both August and September, r < 0.25; P > 0.2; n = 45 in each sample). Thus, ants in the litter appeared to respond directly to substrate moisture, and their numbers were not simply proportional to the amount of litter present at a local site. As a result, ants were distributed independent of topographic position, despite the highly significant (P < .01) difference between the amount of accumulated litter per quadrat at the top of our transect (mean dry mass = 1.2 kg m²) vs. the lower level (mean dry mass = 0.7 kg m²).

Density of ants.—The monthly litter and soil samples collected in 1980 yielded a total of 2573 and 1551 ants, respectively. However, the litter samples encompassed 4.44 times the surface area of the soil samples, so the density of ants per unit area averaged more than 2.5 times as high in the soil as in the overlying litter (Table 4). The combined density of ants in both layers ranged from a minimum of 139 m⁻² in March to a maximum of 1333 m⁻² in June. The relative importance of the two vertical layers also varied markedly from month to month, the litter component of the samples constituting from 10-89 percent of the total ants collected in any given month (Table 4). Some (probably most) of this variation reflected localized vertical migrations of ant colonies, rather than actual changes in numbers. As an example, the 20 soil samples from April 1980 included at least four nests (as judged by the presence of reproductives, brood, or callow workers), whereas the litter samples for that date contained no nests. In contrast, the May 1980 litter samples included a minimum of six nests, the soil samples only one.

DISCUSSION

Distinctiveness of the soil and litter components of the ant community.—The species compositions of the ant assemblages collected in the soil and litter strata were almost identical. Leaving aside the nine rarest species, whose microhabitat associations could not be reliably assessed, the terrestrial ant community at this forested study site consisted of 13 regularly occurring species, all of which were collected in both the litter and the soil layers. Only two of these 13 species showed markedly different relative abundances in the soil vs. the litter (Table 1). *Brachymyrmex depilis*, a tiny (mean dry mass = .06 mg), pale-colored subterranean species with greatly reduced eyes, was much more abundant in

TABLE 2. — Summary of results of stepwise linear multiple regression analysis testing physical factors as predictors of seasonal variation in the abundance of individual ants, species richness and the number of ant species occurrences per five samples. For each of the eight monthly samples, the first 15 sampling stations were combined into three groups of five samples each, giving a total of 24 composite samples for the analysis. In analyses where only one predictor variable was statistically significant (P < .05), values of the simple correlation coefficient (r) and coefficient of multiple determination (r) are given

	Predictor variables		R	R²	P
Response variable	Significant	Nonsignificant	(or r)	(or r²)	
Soil samples					
ln (no. individuals + 1)	Soil temp.	(Soil moisture)	.41	.17	< .05
No. species/5 samples	Soil temp.	(Soil moisture)	.41	.17	< .05
No. occurrences/5 samples	-	(Soil temp.) (Soil moisture)	(.37)	(.13)	NS
Litter samples					
ln (no. individuals + 1)	Litter temp. Litter mass (neg.)	(Litter moisture)	.57	.32	< .05
No. species/5 samples)	Litter temp. Litter mass (neg.)	(Litter moisture)	.67	.45	< .01
No. occurrences/5 samples	Litter temp. Litter mass (neg.)	(Litter moisture)	.58	.34	< .05

the soil (rank = 1) than in the litter (rank = 12). In contrast, *Leptothorax curvispinosus*, another diminutive (mean dry mass = .09 mg), pale-colored species, was the fourth most abundant ant species in the litter samples, but ranked only 12th in the soil samples. The latter species forages extensively in the low arboreal stratum as well as on the ground (Lynch, 1981). Both species depend on homopteran excreta for food, *B. depilis* tending root aphids and *L. curvispinosus* scavenging "honeydew" droplets from leaf surfaces. Thus, *L. curvispinosus* might be considered a surface-feeding analog of the subterranean *B. depilis*.

The remaining 11 species showed similar patterns of relative abundance in both the litter and soil sub-zones (Spearmann rank correlation coefficient = 0.81; P < .01). Seasonal increases of ant activity in one layer tended to compensate decreases in the litter sub-zone, and vice versa. Thus, the between-month coefficients of variation for ant abundance in the litter (CV = 85.2) and in the soil corrected to equal area (CV = 65.9) were substantially higher than the between-month CV for the pooled soil and litter samples (CV = 58.7). However, even these pooled density values showed a broad seasonal peak in abundance (Fig. 3A), perhaps reflecting vertical movements of ants back and forth from depths beyond 10 cm (*cf.*, Headley, 1952; Talbot, 1957) as well as seasonal patterns in mortality and natality.

We conclude that for most ant species in the forest system we studied, the upper 10 cm of soil and the overlying leaf litter are not functionally separated. With few exceptions, the same group of ant species used the soil and litter with about the same relative frequency, although the nature of ant activities (*e.g.*, nesting vs. foraging) may vary vertically in some species. This result contrasts with the relatively sharp vertical segregation between ant species using the litter vs. the low arboreal layers that was previously

TABLE 3.—Summary of results of Model II nested ANOVA testing effects of slope position vs. horizontal patchiness in determining the number of ant species occurrences per litter sample. A similar analysis using absolute numbers of ants, rather than occurrences, showed no significant treatment effects for either of the two monthly samples (P > 0.1)

A. Means and standard deviations (n = 5 replicates per cell)

Elevational Position	Habitat patch within elevation (August 1981)			Habitat patch within elevation (September 1981)		
	1	2	3	1	2	3
Hilltop	2.4(0.9)	3.4(1.3)	4.0(1.6)	0.6(0.5)	2.0(1.2)	2.2(1.6)
Mid-slope	4.0(1.4)	1.2(0.8)	2.0(0.7)	1.0(1.2)	0.6(0.9)	1.6(1.3)
Lower slope	1.0(1.2)	2.8(1.3)	3.8(0.8)	3.4(1.3)	1.0(1.2)	0.4(0.5)
Grand mean	2.7 species/sample			1.4 species/sample		

B. Nested ANOVA's

Source	August 1981			September 1981		
	DF	SS	MS	DF	SS	MS
Total	44	102.8		44	87.0	
Elevation	2	6.5	3.2	2	2.8	1.4
Plots (elevation)	6	47.5	7.9	6	35.3	5.9
Error	36	48.8	1.4	36	48.8	1.4

F(among elevations) = 0.94 (NS)   F(among elevations) = 0.24 (NS)
F(among plots) = 5.84 (P < .001)   F(among plots) = 4.34 (P < .005)

documented at the same site (Lynch, 1981). The observed pattern of vertical movements by ants in response to seasonal and short-term differences in weather is typical of the soil fauna as a whole (Petersen, 1982a).

The soil profile was only sampled to a depth of 10 cm. It is possible that some of the species that were only rarely collected, particularly those with morphological adaptations for subterranean existence (*e.g.*, vestigial eyes, depigmented integument, reduced limb length), reach their maximum abundance below 10 cm, and therefore constitute a distinctive vertical component of the community. However, most such specialists feed either on soil arthropods (*e.g.*, *Proceratium* spp., *Amblyopone pallipes*) or on root-feeding homoptera and their exudates (*e.g.*, *Acanthomyops* spp., *Lasius umbratus*). It therefore seems unlikely that their vertical distributions would be centered much below the superficial root zone. Headley (1952) and Talbot (1957) found that nests of most of the smaller species of terrestrial woodland ants were located within a few cm of the surface, as is also true of soil arthropods as a whole (Petersen, 1982a).

Finally, there are several fairly common local ant species that forage on the forest floor, but occurred only infrequently in our samples. In most instances, undersampling was due to these species having specialized nesting habits or unusual activity patterns, or both. As an example, *Prenolepis imparis*, one of the three commonest surface-foraging species at our study site during spring and autumn (Lynch *et al.*, 1980), typically places its scattered nests 0.5-1.5 m underground (Headley, 1952; Talbot, 1957), and is virtually absent from the surface during midsummer. *Camponotus ferrugineus*, a large surface-foraging species, shows a nocturnal peak in its daily activity (Lynch *et al.*, 1980), and lives in scattered colonies that are located in fallen logs, stumps or standing trees. Adequate sampling of such nest sites, which are also used by such local species as *Camponotus pennsylvanicus*, *C. caryae*, *Aphaenogaster fulva* and *A. tennesseensis*, all of which were relatively poorly represented in our collections, would require specialized (and destructive) collecting methods. Our 1980 sampling progrom did, however, yield an adequate profile of the commoner ant species that utilize the litter and soil sub-zones for nesting as well as foraging. Indeed, analysis of the 90 litter samples collected in 1981, together with an additional 150 litter samples that had been collected in the same forest in 1975-1976 (Lynch, 1981), added only three ant species to the 1980 total.

Effects of physical factors on ant activity. —This study reinforces earlier conclusions (*e.g.*, Sanders, 1972; Markin *et al.*, 1974; Lynch *et al.*, 1980; Lynch, 1981) that temperature is the key determinant of seasonal activity by ants in moist temperate-zone habitats. As

TABLE 4. — Number of species, density (individuals m^{-2}) and biomass (mg dry mass m^{-2}) in eight monthly samples of soil and litter, based on analysis of 20 soil cores (total surface area = 0.36 m^2) and 20 litter samples (total surface area = 2.0 m^2) each month

Month	Soil			Litter			Combined		
	Spp	Density	Biomass	Spp	Density	Biomass	Spp	Density	Biomass
March	6	106	26.0	6	33	1.4	9	139	27.4
April	8	892	137.9	9	70	13.6	10	962	151.5
May	14	239	53.1	11	231	56.4	15	470	109.5
June	11	1106	258.4	13	227	56.8	13	1333	315.2
July	12	656	67.4	11	106	17.4	13	762	84.8
August	7	403	70.5	11	294	31.8	14	697	102.3
September	8	556	60.5	9	114	19.0	9	670	79.5
October	5	325	290.3	7	13	2.4	7	331	292.7

was also found in an earlier study conducted at our Maryland study site (Lynch *et al.*, 1980), a given temperature increment had a greater effect on ant activity early in the activity season than later on. On any particular day and at a given vertical location, all microsites within the closed-canopy woodland we studied, experienced relatively similar temperatures. Under such conditions horizontal partitioning of ant species based on differing thermal requirements would appear to be impossible. This is not the case in open habitats, where direct insolation often produces a well-defined thermal mosaic, to which ants readily respond (*see* summary by Brian, 1983).

Unlike substrate temperature, substrate moisture showed substantial within-habitat horizontal variation on a given day, and was correlated with differences in the abundance and species richness of ants. However, because mean substrate moisture levels remained relatively high (at least in the litter sub-zone) for most of the 8-month study interval, there was little evidence of an independent role for substrate moisture in controlling seasonal (as opposed to microgeographic) differences in ant abundance or species richness. Different results would be expected in habitats such as deserts (*e.g.*, Whitford, 1978), where both temperature and moisture strongly limit ant activity, or in tropical forests with distinctly seasonal rainfall patterns. In a study conducted by Levings and Windsor (1984) at Barro Colorado Island in Panama, litter moisture ranged from 15-25% during the winter dry season, a period of relatively low ant activity. During the wet season, litter moisture at Barro Colorado increased to 45-60% values observed in our Maryland study only in March, when low temperature curtailed ant activity. However, at our study site litter moisture remained above 30% during all but 1 month of the 8-month activity season. Given that temperate-zone sites are characterized by lower potential evapotranspiration rates than are lowland tropical locations, the amount of moisture available in the litter stratum at our study site probably did not greatly curtail seasonal activity of ants for most of 1980. Substrate moisture might, however, play a more important role in years of severe spring or summer drought.

The negative correlation observed between ant abundance and litter mass in 1980 is almost certainly an artifact, reflecting the fact that standing litter mass is lowest in summer, when temperature (and ant activity) is high (Fig. 2B). In effect, the variable "litter mass" served as an indirect indicator of midsummer conditions in the regression analysis. An independent role of season (as opposed to temperature) as a predictor of ant activity was found in an earlier study (Lynch *et al.*, 1980). Litter mass had no independent effect on ant density in either the August or the September samples for 1981.

Ant density and biomass. —There are surprisingly few published data on the abundance or biomass of ants in temperate forested ecosystems (for summaries, *see* Brian, 1978; Petersen, 1982b). The highest observed abundance values are not from forests, but from heathlands and grasslands, where densities as high as 5000-7000 individuals m^{-2} and biomasses as high as 1900-2400 mg dry mass m^{-2} have been reported (Brian, 1978; Petersen, 1982b). For temperate forests, the highest reported ant density in the soil/litter zone appears to be 600 m^{-2}, a figure computed by Baroni-Urbani and Pisarski (1978) from data reported by Talbot (1957) for a mixed hardwood forest in Missouri. The highest colony density so far documented for a temperate forest site is 9 colonies m^{-2}, which was reported by Headley (1952) for a successional locust woodland in Ohio. The density of individual ants was not determined in that study. For comparison with data on colony density presented by Headley (1952), Talbot (1957) and Francoeur (1965, 1966), who have published the only such information for entire communities of North American woodland ants, we computed the minimum number of colonies present in the 90 litter samples collected in mid-August and early September 1981. These samples, which encompassed a total surface area of 9 m^2, contained part or all of 54 nests, as judged by the presence of reproductives or brood, or both. The eight species whose nests occurred in the litter samples were *Paratrechina faisonensis* (28 nests), *Ponera pennsylvanica* (10), *Brachymyrmex depilis* (4), *Myrmica punctiventris* (4), *Smithistruma ohioensis* (3), *Aphaenogaster rudis* (3), *Leptothorax curvispinosus* (1) and *Lasius alienus* (1). The

overall density of nests within the litter sub-zone in late summer 1981 was 6.0 m^{-2}, a figure that exceeds the total colony densities of 0.6-4.3 m^{-2} found in the combined litter and soil zones of mature hardwood forest sites in Ohio (Headley, 1952), Missouri (Talbot, 1957) and southern Quebec (Francoeur, 1965, 1966). Only the 9.0 colonies m^{-2} value from Headley (1952) for the soil and litter zones of the above-mentioned locust woodland in Ohio exceeds the colony densities reported here. The high colony density observed in our 1981 samples seems all the more remarkable, as we did not include the soil layer in that analysis. Many of the ant colonies found in the studies cited above were in soil, rather than the litter.

Monthly densities of worker ants in the litter during the April-September period of intense ant activity ranged from 70-294 individuals m^{-2}. Equivalent seasonal data are not available for the litter zone of other temperate forests, but the study of Levings (1983) in Panama permits a tentative tropical-temperate comparison. The median density of ant workers in the litter zone of mature moist tropical forest on Barro Colorado Island ranged from 70-316 m^{-2}, depending on season (wet vs. dry), and to a lesser extent on the structure and floristic composition of the forest. The leaf litter at our Maryland study site thus supported a similar density of ants to that at the Barro Colorado site during seasons of moderate to high ant activity. An earlier study at the Maryland site (Lynch, 1981) showed that ant density in the litter zone declined to about one individual m^{-2} during the winter months, so ant density is far lower there than at Barro Colorado during several months of the year.

The density of ants in the soil has not yet been studied at Barro Colorado, and we do not know whether the relative importance of the litter and soil strata is similar in tropical and temperate forests. Total ant density therefore cannot be compared at the Maryland and Panama sites. We can note, however, that the pooled monthly mean density values for combined soil and litter ants at our Maryland study site (470-1333 m^{-2}) are comparable with the maximum density value of fewer than 1000 m^{-2} reported for the combined soil and litter subzones of tropical forests by Petersen (1982b).

Given the much higher number of ant species present in tropical habitats, the observed similarity in ant density is somewhat surprising. Levings (1983) collected a total of 108 species of litter-dwelling forest ants in her study at Barro Colorado, whereas a roughly equivalent sampling effort at our Maryland site (combining litter sampling data from 1975-1976, 1980 and 1981, as described above) yielded only 25 ant species in 400 samples totalling 40 m^2 of litter. It is not known whether the presence of similar numbers of ant workers in the soil/litter zone at tropical and temperate sites during seasons of high activity implies a similar ecological impact by ants. Jeanne (1979) found that ants in a Costa Rican forest removed experimentally offered wasp larvae about three times as fast as did ants in a Florida forest, an observation that suggests a greater impact of scavenging ants in the tropics. However, forager activity and food preferences vary substantially among seasons and habitats, and many surface-foraging ants in the tropics actually nest in the tree canopy (J. Trager, pers. comm.), where the species diversity and abundance of ants can be phenomenally high. As a examples, Wilson (1987) identified 43 ant species, belonging to 26 different genera, in a sample collected from a single tree in the Amazonian forest of Peru, and Erwin (1983) reported that ants constituted 42% of the total canopy insects in a sample of more than 24,000 individuals collected in Brazilian rain forest. Much more fieldwork will be required if we are to understand the relative importance of terrestrial vs. arboreal ants as a function of latitude.

As is true of our values for worker and colony density, the biomass values computed for the present study (80-315 mg dry mass m^{-2}) are surely underestimates, for we did not sample deeper than 10 cm in the soil nor did we adequately assess species that nest in logs and stumps (*see* above). Nevertheless, the density and biomass figures reported here are among the very highest that have been reported for ants in forested ecosystems (Peterson, 1982b).

In conclusion, we have demonstrated that most individual ground-dwelling ants in a

temperate deciduous forest community are present in the soil layer, rather than in the litter, during much of the season of activity. As a result, studies based on litter samples alone will greatly underestimate overall ant density, although there were few qualitative differences between the ants inhabiting soil vs. litter. At our Maryland study site, most observed seasonal fluctuations in ant numbers probably reflected local vertical movements rather than mortality/natality. Temperature appeared to be more significant than moisture as a determinant of seasonal changes in ant activity, but the mosaic of ant occurrences at any given time within the April-September season of activity was significantly correlated with horizontal differences in litter moisture. Activity was unrelated to topographic position within the forest except for floodplain habitat. The soil and litter zones of our Maryland study site support a reasonably diverse assemblage of terrestrial ants for a temperate-zone locality (at least 25 species), but the soil/litter community was numerically dominated by a very small number of species. Dominance was especially marked in the litter layer, where a single species (*Paratrechina faisonensis*) accounted for ca. 70% of the individual ants collected. The density of terrestrial ants at our study site is very high, and rivals or exceeds values that have been reported from other temperate and tropical forest ecosystems.

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