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Analysis of the leaf litter arthropod fauna of a lowland tropical evergreen forest site (La Selva, Costa Rica)

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Abstract: Leaf litter arthropod population changes were monitored by means of extensive can trapping over a thirteen month period at a lowland evergreen forest site in Costa Rica. Samples were taken within an undisturbed forest plot and an adjacent fallow cacao plantation. Comparisons of abundance were made between nocturnal and diurnal samples as well as between months. The dominant arthropod groups in the samples in order of abundance were the Formicidae, Apterygota, Orthoptera and Arachnida. Total numbers of individuals in all major groups were consistently greater in the initial stages of the rainy season and remained relatively constant throughout the remainder of the year. It is suggested that numbers increase in response to the onset of the rainy season. Greater numbers of individuals were collected in the undisturbed forest than the fallow cacao plantation. Significant diel differences in abundance were found for many of the major groups included in the study. Maximum arthropod abundance corresponded to the time of greatest leaf litter depth within the study plots.

Historically, studies of tropical arthropods have been qualitative and descriptive in nature (Allen, 1926; Davis, 1945; Strickland, 1945). More recently, insect abundance has been studied by many workers, concentrating on the understory and canopy (Janzen, 1973; Montgomery and Lubin, 1979; Buskirk and Buskirk, 1976). Though the litter floor has begun to receive more attention (Anderson, 1975; Elton, 1973; 1975), most studies have concentrated on individual taxa, in particular beetles, mites, and spiders (Meijer, 1974; Baars, 1979; Mitchell, 1963; Stanton, 1979; Uetz and Unzicker, 1976; Uetz, 1979; Hanlon and Anderson, 1972). Bigger (1976) documented the existence of oscillations in tropical insect populations in general, and considered predator-prey relations to be a causative factor. Wolda (1977; 1979) has shown seasonal fluctuations in tropical insect populations that may relate to rainfall and food abundance.

In this report we evaluate seasonal and diel variation in arthropod abundance of tropical forest leaf litter, based on multiple monthly pit trap samples. Additionally, differences in arthropod abundance between undisturbed forest and disturbed forest planted in cacao are analyzed. The potential relationship between arthropod numbers and rainfall patterns is also examined.

MATERIAL AND METHODS

The study area was Finca La Selva, Heredia Province, Costa Rica. This area is a lowland evergreen wet forest (Holdridge, 1967) at an altitude of 60 m, with a mean annual rainfall of 3969 mm. Two dry months of January-February usually average less than 200 mm rainfall, while the wet months of March-December average more than 200 mm. The study was carried out at two sites: one in a relatively undisturbed forest remnant, the other in an adjacent plantation that was once planted with cacao trees for agricultural purposes but has been fallow for at least 20 years.

The arthropods were trapped using a series of one gallon pit traps. The pit traps were laid out at 10 m intervals in two transect lines, one in undisturbed forest, the other in the cacao plantation. Each trap had a top that could be removed during trapping operations, and contained picric acid solution to fix all specimens at time of capture. Traps were operated at both plots once a month for a period of 13 months, from February 1974 to February 1975. Sampling spanned a continuous four-day period in each of the 13 months. The traps were cleared every 6-10 hours day and night (mean sampling period: 9.02 ± 3.7 hours), the picric acid was replaced, and the arthropods removed and preserved.

In the laboratory, can trap samples were evaluated. Each sample was recorded with respect to numbers of various arthropod groups and their respective sizes. Most arthropods were classified to order (Table 1). Ants were separated from other Hymenoptera; arachnids were

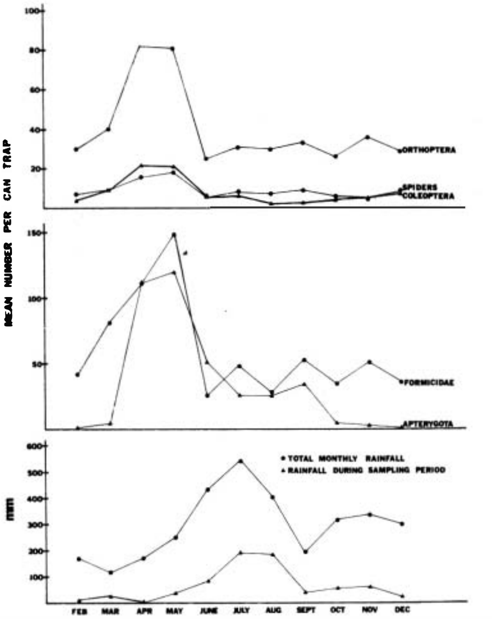

Fig. 1 Seasonal abundances of predominant arthropods and rainfall patterns for the same period.

divided into spiders, mites, and other arachnids. Chilopoda and Diplopoda were placed together, as were snails, worms, and leeches (all relatively uncommon). Though snails, worms and leeches are not arthropods, they were the only other invertebrates found and were thus included. The larvae were initially separated into Diptera, Lepidoptera, Coleoptera, other identifiable larvae, and unidentifiable larvae. The data base for the separation was too small, and no significant differences between them were found. Consequently all larvae are grouped together throughout the paper. The miscellaneous category includes Ephemeroptera, Neuroptera, and Lepidoptera. The unidentified category includes all arthropod individuals that could not be accurately identified.

RESULTS

A total of 21,944 individual arthropods were collected, of which 34.8% were ants, 22.7% Orthoptera, 18.0% Apterygota, 5.0% spiders, and the remaining 19.5% was comprised of all other groups combined.

Figure 1 shows the average numbers of individuals collected per months for the major groups. Total monthly rainfall and rainfall during the sampling periods are also presented. Numbers for all major groups peaked in spring and subsequently declined in summer. With the exception of the Apterygota, numbers remained relatively constant over the remainder of the year. Apterygota exhibited a further decline in numbers in late fall and winter.

More individuals were trapped during the day among the Apterygota, Diptera and the Miscellaneous group, than at night. More individuals were trapped at night than during the day among the ants, spiders, Isopoda, other arachnids, and Chilopoda and Diplopoda. Furthermore, more individuals were found in the forest plot than in the cacao for the Orthoptera, spiders, and Homoptera. Table 1 lists the results of multiple analyses of variance for each arthropod group's abundance. The three factors in the analyses of variance were months of the study, forest versus cacao site, and day versus night. The purpose of such anovas is to test if there are significant effects due to any of these factors, and to test if there are any interactions between the factors. The table lists the probability that there is a significant effect; probability values greater than .05 are not listed and are not considered significant. The three-way multiple anova used allowed for an adjustment for unequal sample sizes. The condition of homoscedasticity was met.

Significant effects exist for month of trapping for all arthropod groups except larvae, miscellaneous, and unidentified (all very rare).

Except for the Hemiptera (p = .006), Isoptera (p = .03), and the Dermaptera (p = .007), these effects are significant at the .0001 level or better.

Interactions between sampling month and forest versus cacao occur in the following groups: Orthoptera, mites, Isopoda, Coleoptera, Apterygota, Homoptera, Hemiptera, and Isoptera. Interactions also occur between month and time of day for ants, Orthoptera, Diptera, Isopoda, Coleoptera, Apterygota, Arachnida, Homoptera, Hemiptera, and Dermaptera. For many groups, the difference between day-night abundances depends on the month (and possibly the associated rainfall). For other groups, the differences between abundances in the forest versus cacao plots also depend on the month of the year. Three-way interactions between month, forest-cacao, and day-night occur only for the Apterygota and the Homoptera.

Figure 2 represents the results of Duncan's multiple-range *a posteriori* test. This test was run subsequent to the three-way multiple anovas on all abundance variables for which there was a significant effect due to month. In Figure 2, lines connect those months for which the means (average abundance of the group) are not significantly different at the .05 level.

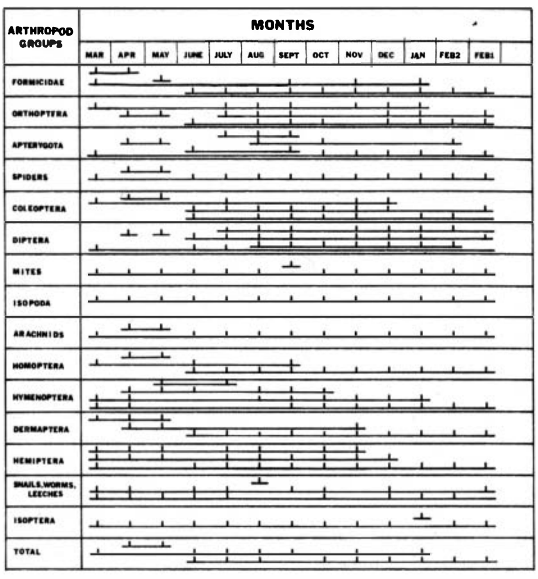

Fig. 2. Results of Duncan's Multiple Range *a posteriori* test. Bars connect those months for which there is no significant difference between the mean abundances of the particular arthropod group.

For ants, the average abundance in May is significantly different from all other months; March and April form a cluster, as do March, September, November, and the following January. Some taxa have only two groups of months that cluster (e.g. spiders and mites), while others evince a greater complexity, with up to five such clusters (Diptera, Apterygota).

Figure 3 relates directly to Table 1. The abundances in the forest and cacao plots, separated into day and night collections, are tabulated. They are tabulated only for those arthropods with significant effects due to either the forest-cacao factor, the day-night factor or both.

Table 2 represents the Pearson product-moment correlations between the numbers of individuals of the arthropod groups. Those correlations significant at the .001 and .0001 levels are indicated. Such stringent significance levels were deemed necessary due to the large sample sizes.

DISCUSSION

Many studies have shown that pit traps (also called can traps or pitfall traps) are the most efficient way of collecting litter arthropods and evaluating their abundances over time (Baars, 1979; Meijer, 1974; Mitchell, 1963; Uetz and Unzicker, 1976). Specifically, Meijer (1974) and Denboer (1971) have found pit traps to be very successful as measures of relative abundance and particularly useful in comparing populations in different sites, even though trap efficiency varies from species to species and habitat to habitat (Mitchell, 1963).

Baars (1979) cautions that many traps are needed in micro-spatially heterogeneous habitats. The large sample size in this study reflects this consideration. The numbers recorded in this study must be viewed comparatively; i.e. some arthropod groups may be sampled more completely than others, but this selectivity will presumably be the same for forest and cacao and for day and night. Previous studies (Baars, 1979; Meijer, 1974; Uetz and Unzicker, 1976) have used smaller pit traps (approximately 0.8 liter). It should be emphasized that this study used one gallon (3.8 liters) pit traps, thus increasing the size of the sample, and presumably the efficiency as well.

Monthly differences: As seen in Figure 1, rainfall begins to increase in May and June and

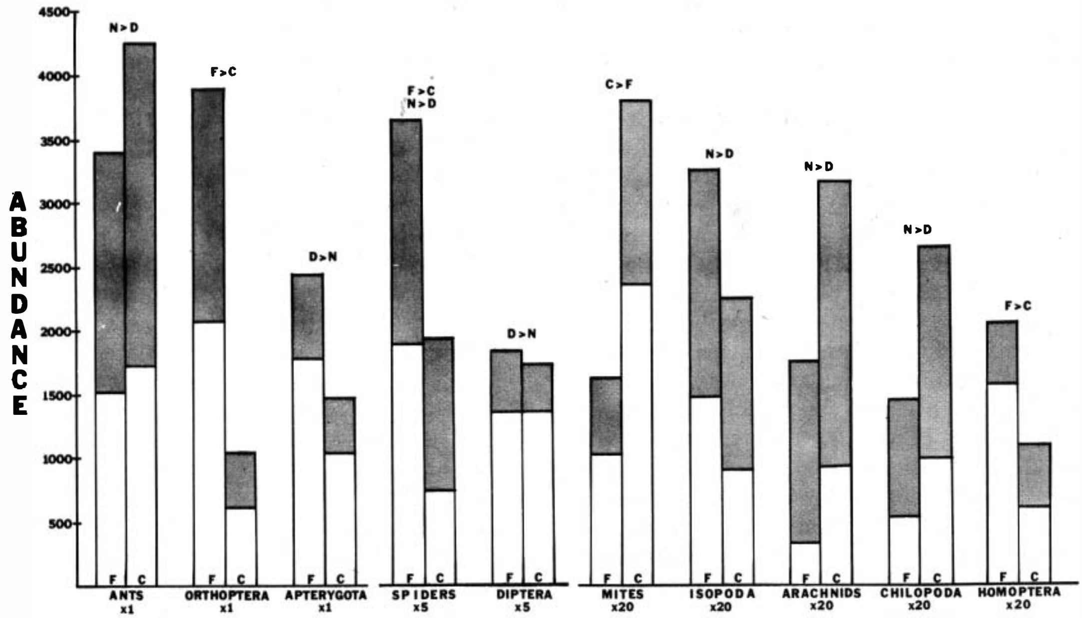

Fig. 3. Total abundance of arthropod groups, separated into forest (F) and cacao (C) sites. Shaded portions are during the day. Only arthropod groups with significant effects due to either the forest-cacao or day-night factors, or both, are included. Those effects that are significant at the 0.5 level are indicated above the individual histograms.

peaks for the sampling period in July and August. Numbers of all major groups of insects reach a maximum between the onset of the rainy season and the period of peak rainfall. While a causal relationship cannot be proven, a correlation between the onset of the rainy season and insect abundance is indicated.

The peak rainfall months of July and August show no significant difference in insect abundance from subsequent drier months for many arthropod groups (ants, Orthoptera, spiders, for example). Notably, it is the non-arthopods, the snails, worms, and leeches, that have a significantly different abundance in August; these are the groups that are likely to do particularly well in wet areas. The two Februaries share a common group of non-significantly different means for all insect groups, suggesting that the year studied is generalizable to other years.

Bigger (1976) has shown cyclical behavior of insect populations over several years. Though our data are insufficient to generalize an annual pattern, a striking monthly variation in arthropod abundances has been shown. Others have shown comparable responses in tropical forest ecosystems. Buskirk and Buskirk (1976), working with sweep samples in a lower montane rain forest (also in Costa Rica), found maximum insect abundance late in the dry season and early in the rainy season. Wolda (1979), working with light traps in Panama, also found a large decrease in insect abundance during the dry season. Denlinger (1980), using Malaise traps in Kenya, found a complex relationship between rainfall and abundance, with the peak of abundance coincident with maximum rainfall.

Several factors influencing the response of insect populations to the onset of the rainy season have been postulated. The increase in insect populations may be due to the heightened availability of plant food (Buskirk and Buskirk, 1976; Wolda, 1979). Work in progress concerns various biotic and abiotic factors which were measured concurrently with the can trap samples. These include temperature, rainfall, and numerous vegetation variables. Following analyses of variance it was found that among the vegetation variables, only leaf litter depth varies significantly with month. Specifically, litter depth is greatest in May and least in October and November. Herbaceous cover appears to be greatest in March and April, and least in November and December (though

TABLE 1

Three-way multiple analyses of variance. The three factors are month (13 levels), forest or cacao (2 levels), and day or night (2 levels). Listed below are the probabilities that the effects are significant for these three factors and their interactions (*). If P ⩾.05, the probability is not listed. FC is forest cacao, and DN is day-night.

VARIABLES[1]	MONTH	FC	DN	MONTH *FC	MONTH *DN	FC*DN	MONTH FC*DN
Total	.0001	.0001	-	.0004	.0001	-	-
Ants	.0001	-	.0001	-	.0395	-	-
Orthoptera	.0001	.0001	-	.0001	.0001	-	-
Spiders	.0001	.0001	.0073	-	-	-	-
Mites	.0001	-	.0208	.0204	-	-	-
Hymenoptera	.0001	-	-	-	-	-	-
Diptera	.0001	-	.0001	-	.0001	-	-
Isopoda	.0001	.0183	.0051	.0039	.0005	-	-
Coleoptera	.0001	-	-	.0006	.0273	-	-
Apterygota	.0001	.0001	.0001	.0001	.0001	-	.0001
Chilopoda							
Arachnida	.0001	.0232	.0001	-	.0016	-	-
Larvae	-	-	-	-	-	-	-
Homoptera	.0001	.0004	-	.0196	.0001	-	.0430
Hemiptera	.0056	-	-	.0156	.0009	-	-
Isoptera	.0324	-	-	.0111	-	-	-
Dermaptera	.0007	-	-	-	.0003	-	-
Miscellaneous	-	-	.0147	-	.0013	-	-
Snails, Worms	.0001	-	-	-	-	-	-
Unidentified	-	-	-	-	-	-	-

1 Chilopoda, above, includes both Chilopoda and Diplopoda. Arachnida includes all Arachnids other than spiders. Snails. Worms includes snails, worms, and leeches. The miscellaneous category is explained in the text.

not at the .05 level of significance). Thus, we find that insect populations are greatest when there is more food available, just before and at the onset of the rainy season.

The ability of insect populations to peak in response to the beginning of the rainy season (whether the response is specifically to the vegetation, the rainfall, both, or some other factors) has been postulated to be due to developmental arrest, with environmental parameters triggering the termination of diapause (Denlinger, 1980). This may be happening in the leaf litter at La Selva as well. In the groups studied, it seems far less likely that individuals are migrating in and out of the area.

Forest versus cacao: Mixed cacao plantations are believed to harbor some of the most complex insect communities (Bigger, 1976). However, more individuals were found in the forest plot than in the cacao for the Orthoptera, spiders, and Homoptera. These groups may be particularly sensitive to the effects of environmental perturbations. In the case of mites, more individuals were found in the cacao than in the forest. Perhaps mites are more capable of exploiting perturbed ecosystems. While other groups have more individuals in the cacao than the forest (ants, other arachnids, Chilopoda and Diplopoda), these differences are not large enough to be statistically significant.

Further study is recommended to determine if these groups, as well as the mites, are either related ecologically or are (as a group) better capable of utilizing the resources in a disturbed ecosystem. Conversely, study is also recommended to determine if those groups more abundant in the forest are indeed less capable of exploiting perturbed ecosystems. Indeed, this shift in composition of the leaf litter arthropod

TABLE 2

Pearson product-moment correlations

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1- Formicidae	X	*+	*+			*+	*+	*+		*+	*+		*+	*+		*+				*+
2- Orthoptera		X	*+			*+	*+	*+	*+				*+							*+
3- Spiders			X			*+	*+	*+	*+		+		*+			+				*+
4- Mites				X																
5- Hymenoptera					X															
6- Diptera						X		*+	*+				*+	*+		*+	*+			*+
7- Isopoda							X	*+										*+		*+
8- Coleoptera								X	*+		*+		*+	*+		*+	+			
9- Apterygota									X				*+							*+
10- Chilopoda										X	*+			*+						
11- Arachnids											X			+		+				*+
12- Larvae												X								
13- Homoptera													X	*+		*+	*+			*+
14- Hemiptera														X		+	+			*+
15- Isoptera															X					
16- Dermaptera																X	*+			*+
17- Misc.																	X			
18- Snails, Worms																		X		
19- Unidentified																			X	
20- Total																				X

The variables, above, are the numbers of individuals collected per can trap (n= 138).
The symbols used above are: *+: If $p < .0001$ +: If $p < .001$
In all cases, $r > 0$.

fauna may have implications both in succession and resource management in the tropics.

It should be noted that total abundance is also greater in the forest. This is to be expected in light of the concept that disturbed ecosystems, particularly in the tropics, have fewer available niches, less environmental predictability and greater variability, and subsequent reduced abundance and species richness within and among very different taxa. Research is in progress to assess the ecological differences between disturbed and undisturbed forest ecosystems for leaf litter amphibians and reptiles that prey upon the arthropods in this study.

Diel differences: There were significantly more ants, Isopoda, spiders, and other arachnids at night than during the day, and more Apterygota and Diptera during the day than at night. It seems probable that niche partitioning exists among the arthropods in the forest leaf litter, with respect to time of day.

Ants: Ants are by far the most abundant macro-invertebrates in the leaf litter of this forest. Several workers have noted a comparable dominance and/or preponderance of ants in tropical forest litters and soils (Strickland, 1945; Wolda, 1977; Collins, 1980). Bigger (1976) found 250 species of ants in a cacao forest. Collins (1980), working in Sarawak on the soil macrofauna, found termites (62.2%) and ants (19.7%) to be the most abundant in a lowland site. Our finding of more ants than any other group (34.8%) and only 0.19% termites may in part be due to a soil-leaf litter difference, or possibly an interesting Old World-New World difference. This study further supports the contention that ants are ecological dominants.

Though not statistically significant, the greater abundance of ants in the cacao may be due to the presence of one or more species which thrive in disturbed habitats. For example, *Wasmannia auropuncta* is present in both areas, but does better in disturbed habitats, is more flexible in its requirements, and is a very aggressive species (Roy Snelling, pers. comm.). There are more ants active at night than during the day. It should be noted that day-night differences may relate in part to the possibility that arthropods may better see and avoid traps during the day. Ants collected during the day are larger on the average than those taken at night. Furthermore, no difference exists in ant size between the forest and cacao, suggesting that the same groups are utilizing both habitats. Different groups appear to be foraging at different times of the day. As seen in Table 2, the abundance of ants correlates highly with the abundances of most other groups, with the exception of mites, other Hymenoptera, and Apterygota (and other rarer groups). Ant abundance is seen as an excellent predictor of overall arthropod abundance. Average ant abundance peaks in April and May, with a sharp drop from May to June. As seen in Figure 2, March, April, and May are significantly different from the other months. As in all other arthropod groups, the February values for the two years are not significantly different.

Orthoptera: Orthoptera are the second most abundant leaf litter group. The sampling method used may underestimate very mobile, hopping and flying groups such as Orthoptera. While they may be underestimated, their numbers are great enough for meaningful comparisons. Though there is no difference in Orthoptera abundance between day and night, there is a substantial difference between the forest and cacao. Orthopteran abundance is reduced in the disturbed ecosystem (Fig. 1). Unlike ants and Apterygota, Orthoptera may be less able to tolerate environmental perturbation. Orthoptera also peak in April and May, just prior to the rainiest months.

Apterygota: The third most abundant group is the Apterygota. Their abundance in traps varies greatly, from 0-36 in December-February, to 899-1011 in April-June. Lieberman (1982) has shown Apterygota to be a rare prey item for Amphibians and Reptiles, which may be related to this unpredictable abundance. Apterygota are significantly more abundant during the day than at night, while no forest-cacao difference in abundance exists.

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RESUMEN

Los grupos de artrópodos más frecuentemente capturados con trampas cilíndricas de un galón (3.78 litros) en ambientes de suelo vegetal en un bosque húmedo de tierras bajas de Costa Rica fueron hormigas, ortópteros y colémbolos. Las muestras indican variaciones estacionales significativas en la abundancia de los grupos mayores. Los números de artrópodos fueron mayores entre la iniciación de la temporada lluviosa y el máximo de precipitación. Los colémbolos, moscas y grupos menos comunes misceláneos se capturaron en mayor cantidad durante el día, mientras que las hormigas, arañas, milpiés y cienpiés se colectaron en mayor cantidad durante la noche. Se capturó una mayor cantidad de artrópodos en los ambientes no perturbados que en los habitats modificados de cultivo de cacao. Los grupos más comunes en ambientes no perturbados fueron los ortópteros, arañas y homópteros. Los mayores números de artrópodos corresponden a los espesores máximos de cubierta vegetal durante los trece meses de muestreo.

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