The Distribution and Abundance of Leaf Litter Arthropods in MOFEP Sites 1, 2, and 3

Jan Weaver and Sarah Heyman[1]

Abstract.—In June 1993, we collected 144 leaf litter samples from 36 plots (4 samples/plot) located in MOFEP forest sites 1, 2 and 3. Half of the plots were placed randomly on northeast-facing stands (ELT 18), and half randomly placed on southwest-facing stands (ELT 17). Arthropods were extracted using Tullgren funnels, and then sorted into morpho-species, counted, and measured. Out of 126 usable samples, we found 22 orders of arthropods, 547 morpho-species, 40,000 individuals, and 30 g of arthropod biomass. ANOVA showed richness, numbers, and mass were higher on northeast- than on southwest-facing plots, but diversity was lower. Diversity, and to a lesser extent, numbers and richness, were lower in site 1.

Theoretically, 90 percent of a forest's Net Primary Production returns to the soil. There, microbial and fungal activity break down the organic debris of the forest into nutrients that can be cycled back into the ecosystem. Although capable of performing this operation by themselves, the microbes and fungi are aided by the fauna living in the leaf litter and the top few centimeters of soil. Mites and collembola, whose combined weight may be less than 2 g/m^2 (Cornaby *et al.* 1974) can be directly responsible for 15 to 28 percent of annual litter breakdown, 1 percent of the potassium release, and 12 percent of the calcium release in a forest (Gist and Crossley 1974). Indirectly they may be responsible for much more nutrient cycling because their feeding breaks litter into smaller fragments, increasing the surface area available for decomposition and leaching, and innoculating the litter fragments with fungi and microorganisms that continue the decomposition (Barbosa and Wagner 1989, Gist and Crossley 1974). Seastedt (1984) estimated the indirect effect of invertebrates on litter decay at 45 to 71 percent, depending on the species of leaf litter (dogwood, tulip poplar, or white oak). The dependence of microbes on invertebrates to aid decomposition may be chemical as well as mechanical. The Collembola *Tomocerus* and *Folsomia* have been shown to ingest clay in greater amounts when consuming *Quercus* leaves. The clay apparently detoxifies the polyphenols and increases the rate of microbial decomposition (Coleman and Crossley 1996).

The leaf litter fauna also play an important role in the forest food web. The soil/litter component of the forest contains half again as much carbon as the standing forest. This large carbon reserve, along with the relatively high assimilation efficiency of invertebrates—20 to 90 percent (Coleman and Crossley 1996), enables the development of long food chains in detrital food webs. These long chains, in turn, allow the concentration of nutrients needed by animals higher on the food chain. Sodium increases two to three times between trophic transfers (Coleman and Crossley 1996), and the calcium necessary for vertebrate bones and egg shells is sequestered by Oribatid mites, Millipedes, and snails from their feeding on fungi, and by spiders from their feeding on these organisms. More directly, the density of leaf litter invertebrates positively influences the population density of animals higher on the food chain (Smith and Shugart 1987, Stenger 1958).

OBJECTIVES OF THIS STUDY

We sampled in Missouri Ozark forests to characterize the pre-treatment leaf litter arthropod

[1] Assistant Research Professor of Biology and Senior Research Technician, respectively, Department of Biological Sciences, Tucker Hall, University of Missouri, Columbia, MO 65211.

community of forests undergoing logging as part of the Missouri Ozark Forest Ecosystem Project (MOFEP). By estimating the numbers, mass, richness, and diversity of this community, and by identifying dominant species and studying their distributions, we hoped to establish ecological markers of ecosystem structure. These markers could then be used to evaluate the impact of logging or other disturbances on the ecosystem.

MODIFICATIONS OF THE MOFEP EXPERIMENTAL DESIGN

Because of its high species diversity, large population size, and high variability, the leaf litter community could not be sampled with the same thoroughness over as large an area as other taxa in MOFEP. Consequently, we decided to use a different sampling and analytical approach. Although the MOFEP experimental design consists of three treatments, each replicated three times in nine forest sites, our study uses only three sites; one to investigate each treatment. Without replicating the treatments at the site level, we cannot discuss the forest-level impact of logging on leaf litter communities. However, we will be able to compare pre- and post-treatment samples to see if variability in these communities over time is related to treatment applications.

MATERIALS AND METHODS

Sampling Dates

Leaf litter samples were collected in the first week of June 1993. Although we also collected samples in June 1994 and 1995, we have not completed analysis of those samples. This paper will cover data only from 1993.

Sampling Scheme

Plots were initially randomly located and resampled yearly. There were 12 plots in each of the three sites: six on Northeast (NE)-facing stands (ELT18), and six on Southwest (SW)-facing stands (ELT17). Sample locations are shown in figure 5 of Brookshire *et al.* (1997), a foldout map included with this proceedings. Each plot was 5 x 5 m, and was marked semi-permanently with 25-cm pieces of PVC pipe driven into the ground at the bottom and upper left corners of the plot. In addition, two trees within a few meters of the downhill pipe were marked with paint and their positions relative to the pipe were recorded in case the pipe disappeared. Samples were collected from four randomly selected points within each plot each year (4 x 36 =144 samples total). Sampling was without replacement.

Sampling Protocol

Once the sample point was located, a 3-pound coffee can with a diameter of 15.5 cm (area = 0.02 m^2) was plunged into the litter and pressed down. A sharp knife was used to cut the litter and small twigs from around the can, and this debris was brushed away from the can perimeter. Larger sticks were broken off or gently removed from underneath the can. A gallon-size clear plastic bag with a label indicating date and location of sample was readied, the can was lifted, and the litter was grasped in one hand and then scooped into the waiting bag. Spiders, beetles or cockroaches escaping from within the sample perimeter were stunned by slapping them with a flat palm, and then placed in the bag. All litter down to, but not including, finely divided leaf litter and soil was collected. Stones, large clumps of soil (>10 mm), or sticks (of a size to poke holes in the bag) were not placed in the bag, but were examined for arthropods before being discarded.

Sample Extraction

We used a Tullgren Funnel to extract arthropods from the litter. The extraction equipment consisted of:

1. paint buckets (1 and 2 gallon);
2. a funnel made out of aluminum flashing with a large end diameter of 30 cm, a small end diameter of 3 cm, a length of 20 cm, and an angle of approximately 45°;
3. a circular piece of 1/2 in. hardware cloth 23 cm in diameter;
4. an inverted funnel-shaped lamp support made out of aluminum flashing with a large end diameter of 26 cm, a small end diameter of 22 cm, a length of 18 cm, and four 3.5- x13-cm screened openings in the upper half;
5. a polarized clamp lamp with a white plastic shade from SNAPIT (Leviton Co., Cable Electric Products, Inc., PO Box 6767, Providence RI 02940) fitted with a 25-watt bulb;
6. a 100-ml plastic container filled with 40 ml of 70 percent ethanol.

The plastic container sat in the bottom of the bucket, which supported the funnel, the screen was laid in the funnel, the lamp support was placed large side down in the funnel, and the clamp lamp was placed over the lamp support. The lamp support held the light away from the sample and prevented the larger and more active arthropods from walking out of the funnel. The screened openings in the funnel support helped prevent the sample from becoming too hot. Leaf litter was spread over the surface of the screen before setting it in the funnel.

Samples were processed the day they were collected, usually within 6 hours. Until processing, samples were kept in a Styrofoam ice chest. Leaf litter was unbagged onto the screen while the screen rested on a plate; then the screen was carefully placed in the funnel and litter that had fallen onto the plate was tipped on the piled litter. The leaf litter was heated and dried by the 25-watt bulb suspended 10 to 15 cm above it. The temperature inside the funnel was approximately 40° C. The samples remained in the funnels for 42 to 46 hours. Arthropods moved down through the litter as the sample dried and fell through the screen supporting the sample into the container of 70 percent ethanol.

Sampling Efficiency

To evaluate the efficiency of the Tullgren funnels, one leaf litter sample from each plot (collected in 1995) was hand-sorted under a dissecting microscope after it had been extracted, and the numbers and kinds of arthropods found were recorded.

Sample Analysis

The sample containers were returned to the lab, and the number, length, and morpho-species of individuals over 0.2 mm were determined and recorded. Species identifications were not made; instead, different kinds of individuals were identified by their morphology, or body shape, and given a unique number so that their distribution across samples could be determined. Although specimens are being sent to specialists for ultimate identifications, for the purposes of this work it was sufficient to be able to simply distinguish one kind of morpho-species from another (Oliver and Beattie 1993). The only exception to this generalization is that the Diptera, Coleoptera, and Oribatid mites all have larva that look different from the adult forms, so the richness of these groups may have been overestimated because some species were counted twice. On the other hand, the larval forms usually live in different microhabitats, eat different food, and are eaten by different animals. So although larvae and adults are connected through time, they were functionally different species within the parameters of this study. Individuals less than 0.2 mm were too small and numerous for us to reliably sort them into morpho-species. However, these were sorted into orders and their total numbers were estimated by counting individuals in a subsample.

To keep track of the morpho-species across multiple samples, each new species was sketched and specimens were preserved in a reference collection maintained in our laboratory at the University of Missouri. Individuals in new samples were compared to sketches of previously recorded morpho-species and/or compared to individuals in the reference collection before being assigned to a morpho-species.

The number and length of each morpho-species found in a sample were entered into a computer database. In addition, each morpho-species was assigned a six-letter code that allowed species within a sample to be sorted by taxonomic categories. The first letter of the code designated the phylum, the second the class, the third the order, the fourth the family, the fifth and sixth the genus and species, respectively. The letter Z was used whenever the taxonomic category was unknown. This made it possible to sort the data into various taxonomic categories for further analysis and to update the code for a particular species as identifications were made.

Once data from individual samples were entered, the numbers, mass, richness, and diversity for each sample were determined. Numbers and richness were derived directly by counting the number of individuals and morpho-species in a particular sample. To determine mass, the average length for each morpho-species in a sample was converted to milligrams using regression equations specific to its taxonomic group. This value was multiplied by the number of individuals of that morpho-species, and then masses of all morpho-species in a sample were summed to find the sample mass.

The equations for mite and Collembola mass were determined in our lab by a student technician. Live mites and Collembola were chilled (to reduce movement) and then individually weighed on a Cahn 28 Electrobalance. After checking to make sure the animal was still alive, the technician preserved it in 70 percent ethanol and measured its length using an ocular micrometer. Equations for the other groups were taken from Sage (1982). The number of animals used (n) and the R^2 and probability for each regression are listed with its equation. All equations are for wet/fresh weight with length expressed in mm and mass espressed in mg.

1. Mites ($n = 22$, $R^2 = 0.88$, $p < 0.001$)
   $mass = 10^{(0.99081 + 2.5103 \times \text{Log10 (length)})}$

2. Other Arachnids (spiders, pseudoscorpions, *etc.* $n = 39$, $R^2 = 0.91$, $p < 0.001$)
   $mass = 1000 \exp (0.459 (length) - 0.007 (length)^2 - 6.504)$

3. Collembola ($n = 23$, $R^2 = 0.88$, $p < 0.001$)
   $mass = 10^{(-1.3233 + 2.1211 \times \text{Log10 (length)})}$

4. Other Insects (beetles, ants, bugs, thrips, *etc.* $n = 153$, $R^2 = 0.87$, $p < 0.001$)
   $mass = 1000 \exp (0.369 (length) - 0.004 (length)^2 - 6.973)$

5. Soft Bodied Larvae (ants, flies, moths, butterflies, *etc.* $n = 27$, $R^2 = 0.96$, $p < 0.001$)
   $mass = 1000 \exp (0.355 (length) - 0.004 (length)^2 - 7.622)$

6. Hard Bodied Larvae/Myriapods (beetles, centipedes, millipedes, *etc.* $n = 9$, $R^2 = 0.84$, $p < 0.001$)
   $mass = 1000 \exp (0.735 (length) - 0.16 (length)^2 - 10.783)$

The diversity index used was the inverse Simpson's index, $1/\Sigma pi^2$ (Hill 1973) where pi is the proportion of species i in the sample. Therefore, samples dominated by one or a few species have lower diversities than samples in which individuals are more uniformly distributed among species. Richness, on the other hand, is weighted towards rare species because every species counts the same regardless of whether it is represented by 1 or 100 individuals. All other diversity indices fall somewhere between these two measures (Hill 1973) so they represent the end points of a continuum of diversity measures. Together, the two estimates give a more complete picture of a community's diversity than using a single index.

Plot Data

In 1996, plots were visited to gather environmental data on them. Plot 4 in site 1 and plot 6 in site 2 could not be located during this trip so there are no data from them. The aspect was determined for each plot, as opposed to the aspect of the stand it was in; the percent slope and soil pH were also determined. To measure soil pH, 2 to 5 cc of soil were collected from the center and four corners of each plot and physically mixed in a plastic bag. Then 5 g of soil were mixed with 10 drops of millipore water to make a paste. ColorpHast indicator sticks were inserted into this paste and compared to a standard chart to obtain soil pH.

Data Analysis

We analyzed the distribution and influence of plot aspect (compass orientation), percent slope, and pH on community characteristics and species populations using Pearson correlation with Bonferroni-adjusted family probabilities. To perform correlation analysis on aspect, we converted the azimuth to eight classes: 1(338-22°), 2(23-67°), 3(293-337°), 4(68-112°), 5(248-292°), 6(113-137°), 7(203-247°), and 8(138-202°), with class 1 being the northernmost and class 8 being the southernmost. Although this is not a widely used method of classifying aspect, the categories we selected were adequate to highlight general trends.

We used ANOVA to analyze the distributions of community characteristics and species populations by site and aspect. For aspect, we used both the plot aspect (compass orientation of a plot) and the stand aspect (the compass orientation of the stand a plot was located in). For plot aspect, classes 1 to 4 (293°-112°) were designated NE-facing and classes 5 to 8 (113°-292°) were designated SW-facing. This allowed us to assess the influence of plot environmental conditions vs. stand environmental conditions. We also used ANOVA to check how uniformly the plot variables percent slope and pH were distributed by compartment and aspect.

RESULTS

Forest Floor Arthropods

Of the 144 samples collected in 1993, 18 had to be discarded because they were knocked over, dried out, or contaminated with fungus. However, each plot was represented by at least one sample. The 126 remaining samples contained 40,000 individuals over 0.2 mm in length, had a mass of approximately 30 g, included 547 morpho-species, and had an overall diversity value of 28.1. The average number of individuals per sample was 323, the average biomass was 235 mg, the average richness was 55 morpho-species, and the average diversity value was 15.8. The average number of individuals per square meter was 16,150 (average sample number x 50), and the average mass was 11.7 g/m^2. Because neither richness or diversity increases arithmetically with area, their values per square meter can't be estimated by multiplying the average values by 50.

Figure 1 shows the average number of individuals per square meter, the total mass per square meter, and the total number of morpho-species for each of 22 arthropod taxa found in the leaf litter. Based on numbers alone, the Diptera (adult and larval flies, mostly Cecidomyidae), Collembola (springtails), and Acari (Oribatid, Mesostigmatid, and Prostigmatid mites) were the most important members of the community. If mass were considered, the Hymenoptera (mostly ants), Diptera, Orthoptera (two species of cockroaches), and the Acari were the most important members of the community. If richness were considered, then Diptera, Coleoptera (adult and larval beetles), Aranea (mostly Gnaphosid spiders), and Acari dominated. The overall dominants in the community (at least 50 individuals/m^2, 50 mg/m^2, and 50 species) were the Diptera, Coleoptera, Aranea, Acari, and the Hymenoptera. The Lepidoptera (almost all larval) and Collembola could be considered subdominants.

In our evaluations of sampling efficiency, an average of 18.5 arthropods remained in litter extracted in the Tullgren funnels in 1995. If the average number of arthropods in a 1995 sample is comparable to the average of the 1993 samples, then approximately 5.7 percent of arthropods are missing from the leaf litter samples once they are processed. This percentage of individuals was within the limits of the samples' standard errors for numbers and mass (assuming the average mass of an individual is 1 mg), so we do not believe these missing arthropods affected results for numbers or

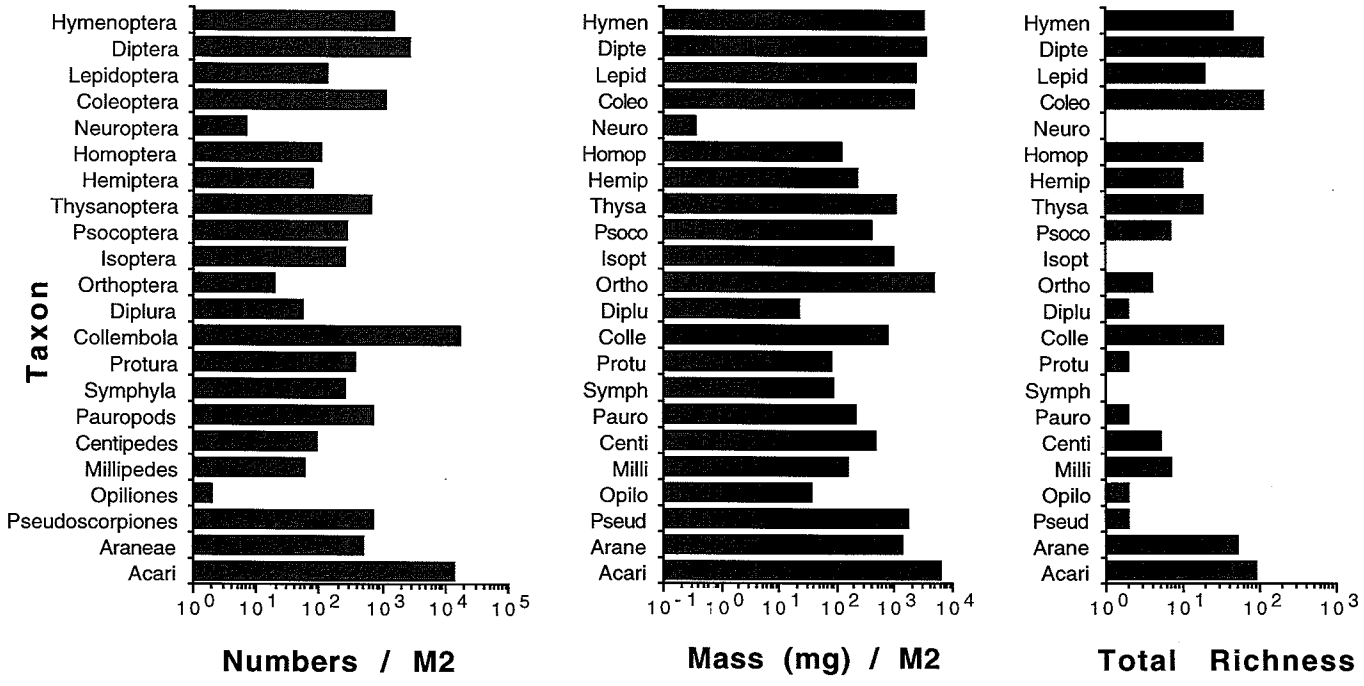

Figure 1.—*Average numbers per square meter, mass per square meter, and total richness for 22 arthropod taxa found in 126 leaf litter samples.*

mass. Richness would be more sensitive to missing arthropods if they also represented missing species, but in most cases, the arthropods were members of a common group. Diversity would be less sensitive, since this measure is weighted more heavily towards common species. Interestingly, there were a large number of snails, about four per sample, a much higher value than we normally found in extracted samples. If this value is representative, a typical square meter of forest floor would have more than 200 snails.

Community Characteristics

Table 1 contains data on aspect(s), slope, and pH for each plot, along with the average (based on 1 to 4 samples per plot) numbers (N), mass (M), richness (R), and diversity (D) of its arthropod community. In eight cases, the orientation of the plot was markedly different from the stand orientation, with four plots shifting from NE to SW and four shifting from SW to NE. Using Pearson correlation coefficients with Bonferroni family probability rates, richness was highly correlated with both numbers ($r = 0.765$, $p < 0.001$, family: N, M , R, D), and mass ($r = 0.443$, $p = 0.041$), but diversity was not correlated with any of the other community characteristics (Wilkinson 1989). Only number was significantly correlated with any of the plot variables—numbers decreased as slope increased ($r = -0.570$, $p = 0.003$, family: N, plot class, slope, pH).

Table 2 contains means and standard errors for community characteristics, plot variables, and 10 numerically dominant species. Data were averages of average sample values for a plot, and represent N, M, R, and D for a 0.02 m^2 sample. There is a set of values for all plots, for NE and SW plots, and for site 1, 2, and 3 plots. The numerically dominant species accounted for 47 percent of the individuals found in all plots; therefore, it is not surprising that overall diversity (28.1) was relatively low compared to the richness (547). From the table, it is clear that NE plots had higher numbers, mass, and richness, but lower diversity than the SW plots. NE plots also had less steep slopes and a higher pH than SW plots. Four of the 10 dominant species, *Onychiurus ramosus, Folsomia stella*, the box mite, and *Hypogastrura brevis*, had at least 1.5 times as many individuals on NE plots as on SW plots, and may account for the higher numbers and mass on NE plots.

There were also marked differences among sites. Site 1 had lower numbers, mass, richness, and diversity than sites 2 and 3. It also had steeper slopes and a lower pH. Of dominant species, it had markedly fewer *H. brevis* and more *Pseudosinella* sp. 367. Site 2 had a higher mass and more *Hypogastrura brevis*, while site 3 was distinguished by having more *O. ramosus*.

These patterns were tested using ANOVA, and the results are shown in table 3. We tried three models: the first included the interaction of site and plot aspect as well as their main effects, the second looked only at main effects of site and plot aspect, and the third used stand aspect instead of plot aspect to examine the relative influence of local (plot aspect) versus general (stand aspect) conditions. Numbers, mass, and richness varied strongly ($p < 0.05$) and diversity varied weakly ($0.05 < p < 0.1$) with plot aspect. There was a weak effect of site on numbers and richness and a strong effect on diversity. There was no interaction between site and plot aspect for the community variables. When the same data were analyzed using stand aspect, differences between aspect became weaker or disappeared.

As a check on the uniformity of the plots' physical and chemical characteristics, we performed ANOVA on percent slope and pH by site and aspect. Slope was steeper on SW plots than on NE plots, and pH was lower in site 1 than in sites 2 and 3. The plot locations were selected randomly so it seems unlikely we happened to randomly locate plots on more steep slopes in SW-facing stands than in NE-facing stands, but it also seems unlikely that SW stands would tend to be steeper. With regard to pH, it is possible that sites or aspects could influence pH. In any case, these differences in physical and chemical characteristics will have to be considered in evaluating treatment differences among plots.

For dominant species, only *O. ramosus*, *Lepidocyrtus* sp. 149, and the box mite showed a strong response to aspect, appearing to prefer NE to SW plots and/or stands, and both *Folsomia stella* and Pseudoscorpiones sp. 97 were weakly responsive to plot aspect. None of the species showed significant differences in distribution with site. The relative lack of response of some species may have been due to the high variability in their distributions. For

Table 1.—*Plot variables and community characteristics for 36 plots. Plot compass, plot aspect, slope, and pH are from June 1996 (except for plots 1.4 and 2.6,which could not be located on that trip). Arthropod numbers, mass, richness, and diversty are from June 1993. Arthropod values are sample averages per plot.*

Site Plot	Stand aspect	Plot compass	Plot aspect[1]	Plot class	Percent slope	pH	# Samples	Number of arthropods	Mass(mg)	Inverse Simpson's Richness	diversity
1.1	S	210	S	7	22	4.0	4	212	77	39	10.9
1.2	N	355	N	1	23	4.5	2	252	180	46	11.4
1.3	N	115	S	6	27	4.5	4	341	113	50	10.7
1.4	S	.	S	.	.	.	4	234	93	43	10.1
1.5	S	105	N	4	35	4.7	2	342	180	63	12.4
1.6	N	270	S	5	36	5.0	4	233	117	50	12.4
1.7	N	330	N	3	26	5.5	4	178	110	43	13.5
1.8	S	205	S	7	48	4.5	4	246	164	52	15.5
1.9	N	10	N	1	30	4.5	4	348	267	63	14.5
1.10	N	30	N	2	25	4.5	4	251	904	55	14.3
1.11	S	190	S	8	33	3.5	4	171	44	37	11.8
1.12	S	150	S	8	45	4.0	4	313	155	61	18.6
2.1	S	190	S	8	30	4.7	4	228	213	51	17.0
2.2	S	120	S	6	20	5.5	4	410	724	64	16.5
2.3	S	85	N	4	20	5.5	4	515	705	60	11.6
2.4	N	315	N	3	24	5.0	4	567	39	63	11.5
2.5	N	2	N	1	12	5.5	4	700	202	73	18.8
2.6	S	.	S	.	.	.	1	304	195	63	19.3
2.7	N	5	N	1	27	4.0	4	428	252	59	15.2
2.8	N	45	N	2	33	5.0	4	274	87	52	17.2
2.9	N	35	N	2	25	5.5	2	321	263	62	16.1
2.10	S	245	S	7	43	5.0	2	156	154	49	21.0
2.11	S	255	S	5	45	5.5	4	126	49	36	13.5
2.12	N	340	N	1	37	6.0	4	279	269	58	18.1
3.1	N	60	N	2	30	5.0	4	390	196	56	10.9
3.2	N	65	N	2	18	5.7	4	448	691	66	12.0
3.3	N	110	N	4	16	6.0	4	433	478	60	6.2
3.4	S	295	N	3	30	4.5	4	390	196	56	10.9
3.5	N	90	N	4	20	5.0	4	293	156	60	22.6
3.6	S	110	N	4	16	5.0	2	457	72	60	17.5
3.7	N	120	S	6	30	6.0	2	477	315	67	18.5
3.8	N	115	S	6	27	5.7	3	207	83	50	18.3
3.9	S	270	S	5	34	4.0	1	243	64	63	25.4
3.10	S	135	S	6	35	5.5	4	321	91	59	20.3
3.11	S	170	S	8	21	5.0	4	297	147	56	18.4
3.12	S	250	S	5	24	4.0	4	249	50	39	13.2

[1]Aspects were grouped into the following classes: 1=338-22°, 2=23-67°, 3=293-337°, 4=68-112°, 5=248-292°, 6=113-137°, 7=203-247°, and 8=138-202°.

Table 2.—*Means and standard errors for community characteristics, plot variables, and numbers of numerically dominant species. Means are for average plot values, (plot values have an area of = 0.02 m²), for all plots, for northeast (NE) and southwest(SW) plots, and for sites 1, 2, and 3. Standard errors are shown in parentheses below each mean.*

Characteristic/Variable		All plots (n = 36)	NE plots (n = 18)	SW plots (n = 18)	Site 1 (n = 12)	Site 2 (n = 12)	Site 3 (n = 12)
Numbers	mean	323	381	264	260	359	350
	standard error	(21)	(30)	(21)	(18)	(49)	(27)
Mass (mg)		235	311	158	200	292	211
		(35)	(55)	(37)	(66)	(62)	(56)
Richness		55	58	51	50	57	58
		(1.5)	(1.6)	(2.3)	(2.6)	(2.7)	(2.2)
Diversty (inverse Simpson's)		15.2	14.1	16.2	13.0	16.3	16.2
		(0.7)	(0.9)	(1.0)	(0.7)	(0.9)	(1.6)
Slope (percent)		28	25	32	31	29	25
		(1.4)	(1.6)	(2.1)	(2.5)	(2.8)	(2.0)
pH		4.9	5.1	4.8	4.5	5.3	5.1
		(0.1)	(0.1)	(0.2)	(0.1)	(0.1)	(0.2)
Onychiurus ramosus (n) Collembola		41.9	54.6	29.3	36.2	38.7	50.9
		(5.2)	(8.0)	(5.2)	(9.0)	(6.9)	(10.8)
Tomocerus lamelliferous (n) Collembola		21.3	22.6	20.1	25.1	22.4	16.5
		(2.6)	(3.5)	(4.0)	(4.4)	(5.9)	(2.8)
Mesostigmatid mite sp. 154 (n)		18.4	18.6	18.1	16.7	18.9	19.5
		(1.4)	(1.9)	(2.1)	(2.2)	(2.4)	(2.7)
Tomocerus elongatus (n) Collembola		15.1	14.7	15.5	13.8	16.4	15.1
		(1.3)	(1.9)	(2.0)	(1.7)	(2.7)	(2.5)
Lepidocyrtus sp. 149 (n) Collembola		13.1	13.5	12.7	13.7	10.4	15.1
		(1.5)	(2.7)	(1.6)	(2.4)	(2.0)	(3.4)
Folosomia stella (n) Collembola		11.3	18.2	4.5	10.8	15.1	8.1
		(3.5)	(6.7)	(1.2)	(3.6)	(9.9)	(2.9)
Oribatid mite sp. 329 (n) (Euphthricaridae - box mite)		8.3	10.1	6.4	6.2	10.2	8.3
		(0.8)	(1.4)	(0.8)	(0.9)	(1.9)	(1.4)
Hypogastrura brevis (n) Collembola		8.1	11.6	4.6	2.6	15.8	5.9
		(2.8)	(5.3)	(1.3)	(0.6)	(7.8)	(1.8)
Pseudosinella sp. 367 (n) Collembola		7.6	8.0	7.2	10.0	6.9	5.9
		(0.9)	(1.3)	(1.4)	(1.4)	(2.0)	(1.3)
Pseudoscorpiones sp. 97 (n)		5.6	6.6	4.6	4.8	5.6	6.5
		(0.5)	(0.7)	(0.8)	(0.9)	(0.8)	(1.2)

Table 3.—*ANOVA of community characteristics, plot variables, and dominant species on compartment and aspect. Weakly significant values (0.05 < p < 0.10) are underlined, strongly significant values (p < 0.05) are underlined and set in boldface. F-values and p-values are ordered for site, aspect, and site x aspect effects as indicated in the first entry of the table.*

Variable		Model 1		Model 2		Model 3	
		Site	df = 2	Site	df = 2	Site	df = 2
		Plot aspect	df = 1	Plot aspect	df = 1	Stand aspect	df = 1
		S x PA	df = 2	Error	df = 32	Error	df = 32
		Error	df = 30				
Numbers	Site	F = 2.7	p = 0.085	F = 2.3	p = 0.115	F = 2.7	p = 0.080
	Aspect	F = 9.7	p = **0.004**	F = 9.1	p = **0.005**	F = 3.1	p = 0.089
	S x A	F = 2.0	p = 0.147				
Mass (mg)		F = 0.5	p = 0.610	F = 0.4	p = 0.645	F = 0.7	p = 0.515
		F = 4.4	p = **0.045**	F = 4.5	p = **0.041**	F = 1.8	p = 0.188
		F = 0.6	p = 0.573				
Richness		F = 2.4	p = 0.108	F = 2.6	p = 0.088	F = 3.1	p = 0.061
		F = 5.0	p = **0.033**	F = 5.2	p = **0.029**	F = 2.6	p = 0.117
		F = 0.2	p = 0.815				
Diversity (Inverse Simpson's)		F = 3.3	p = 0.052	F = 3.6	p = **0.039**	F = 2.8	p = 0.078
		F = 4.0	p = 0.054	F = 3.9	p = 0.058	F = 0.9	p = 0.353
		F = 2.1	p = 0.146				
Slope (percent)		F = 1.6	p = 0.224	F = 1.6	p = 0.216	F = 1.6	p = 0.213
		F = 6.5	p = **0.016**	F = 6.9	p = **0.013**	F = 3.2	p = 0.083
		F = 0.1	p = 0.920				
pH		F = 4.7	p = **0.017**	F = 5.1	p = **0.012**	F = 7.5	p = **0.002**
		F = 1.6	p = 0.215	F = 1.7	p = 0.204	F = 8.7	p = **0.006**
		F = 0.2	p = 0.835				
Onychiurus ramosus (n)		F = 0.9	p = 0.426	F = 0.9	p = 0.424	F = 0.9	p = 0.414
		F = 6.7	p = **0.015**	F = 6.9	p = **0.013**	F = 7.5	p = **0.010**
		F = 0.5	p = 0.612				
Tomocerus lamelliferous (n)		F = 0.7	p = 0.487	F = 0.9	p = 0.404	F = 0.9	p = 0.419
		F = 0.3	p = 0.594	F = 0.3	p = 0.599	F < 0.1	p = 0.829
		F = 2.6	p = 0.091				
Mesostigmatid mite sp. 154 (n)		F = 0.3	p = 0.731	F = 0.4	p = 0.707	F = 0.4	p = 0.700
		F < 0.1	p = 0.950	F < 0.1	p = 0.947	F < 0.1	p = 0.893
		F = 0.1	p = 0.940				
Tomocerus elongatus (n)		F = 0.3	p = 0.752	F = 0.3	p = 0.718	F = 0.3	p = 0.745
		F = 0.2	p = 0.684	F = 0.2	p = 0.682	F = 0.3	p = 0.573
		F = 1.8	p = 0.186				
Lepidocyrtus sp. 149 (n)		F =0.9	p = 0.429	F = 0.8	p = 0.438	F = 0.9	p = 0.408
		F = 0.1	p = 0.730	F = 0.1	p = 0.721	F = 4.5	p = **0.042**
		F = 1.7	p = 0.197				
Folsomia stella (n)		F = 0.2	p = 0.824	F = 0.2	p = 0.785	F = 0.3	p = 0.720
		F = 3.5	p = 0.071	F = 3.6	p = 0.066	F = 2.5	p = 0.125
		F = 0.4	p = 0.688				
Oribatid mite sp. 329 (n)		F = 1.4	p = 0.258	F = 1.6	p = 0.223	F = 2.6	p = 0.093
		F = 4.5	p = **0.042**	F = 4.1	p = 0.051	F = 11.2	p = **0.002**
		F = 2.2	p = 0.129				
Hypogastrura brevis (n)		F = 1.7	p = 0.199	F = 1.9	p = 0.166	F = 2.1	p = 0.134
		F = 1.2	p = 0.279	F = 1.1	p = 0.305	F < 0.1	p = 0.851
		F = 2.3	p = 0.118				
Pseudosinella sp. 367 (n)		F = 1.6	p = 0.225	F = 1.8	p = 0.180	F = 1.7	p = 0.200
		F = 0.3	p = 0.559	F = 0.4	p = 0.553	F < 0.1	p = 0.898
		F = 1.9	p = 0.172				
Pseudoscorpiones sp. 97 (n)		F = 0.8	p = 0.444	F = 0.8	p = 0.473	F = 0.8	p = 0.449
		F = 3.3	p = 0.077	F = 3.3	p = 0.078	F = 0.9	p = 0.358
		F = 1.5	p = 0.239				

example, although *Hypogastrura brevis* was more than twice as abundant in site 2 than in 1 and 3, and on NE than on SW stands, its standard error values were 23 to 49 percent of the mean value.

DISCUSSION

Although there is a large and varied literature on leaf litter communities, we have as yet found no studies directly comparable to ours with respect to the ecological community investigated, the methods used, and the members of the community sampled. Hoekstra *et al.* (1995), sampling leaf litter communities in coastal redwood, found 11,500 individuals/m^2 in old-growth forest, 22,000 individuals/m^2 in mature second-growth forest, and 3,500 individuals/m^2 in cut forest (these values for area were derived from their volume estimates). These numbers are comparable to the 16,150 individuals/m^2 we estimate are present in our second-growth Ozark forest. Seastedt and Crossley (1981), sampling in Appalachian forest, found 98,900 to 133,500 individuals/m^2. However, their samples included soil as well as litter, and they counted animals smaller than 0.2 mm, which we did not. We did estimate the number of individuals in this size class for all our samples and adding them would easily double our population estimates. This still does not put us in the range of Seastedt and Crossley's numbers, but their inclusion of soil as well as litter might account for the difference. Moulder and Reichle (1972) estimated the macroarthropod density in oak forest at 514/m^2. They also estimated biomass at 8.6 g/m^2. A similar suite of taxa from our study gave values of 2,212 individuals/m^2. Because Moulder and Reichle were investigating spider prey, it is likely that we included more small individuals than they did, so our population estimate would be larger. Their estimate of mass, however, is roughly consistent with ours, 11.7 g/m^2. We found no estimates of richness for the total arthropod community, though several studies estimated richness for particular groups.

The significant correlation between richness and mass that we found in our community is consistent with Tilman (1996) and Tilman *et al.'s* (1996) finding that in grassland communities, plant mass and productivity (but not numbers) are increased by species richness of the plant community. The authors hypothesize that increased richness increases the redundancy in the system, allowing different plant species to exploit variability in local conditions over time while ensuring constancy of primary production and therefore of plant biomass. Didham *et al.* (1996) make a similar argument for the decomposer community of the forest floor. Decomposition is only weakly related to numbers but can experience dramatic declines when richness decreases. A large number of leaf litter arthropod species may mean that all or most of the available niches and microhabitats are being utilized, thus increasing the transfer of resources from microbes and fungi to arthropods. When particular species are lost, their niches are no longer used, and resources in the food chain may be routed through other channels in the community, including being leached into lower soil layers where they may no longer be available to any members of the community. A similar argument may account for the relation of richness to numbers.

The lack of correlation between diversity and any of the other community characteristics in our study was rather surprising. Tilman and Tilman *et al.* found their diversity measures (like the Shannon-Weiner index) correlated with mass. The discrepancy could be due to the different communities investigated, the different taxa sampled, or to our use of the inverse Simpson's index. What our results do suggest is that the factors that dictate how evenly resources are shared differ from the factors that dictate how many species there are. For example, extreme environmental conditions, like drought, flooding, soil pH, percent slope, or even a food-rich environment will be advantageous to the particular species adapted to them. These species will garner a larger share of the available resources, effectively reducing evenness and therefore the value of the inverse Simpson's index. However, these extreme conditions might not be severe enough to actually exclude other species, which might continue at very low population levels. Thus, richness would remain relatively constant while diversity went down.

Only numbers correlated significantly with any of the physical/chemical characteristics of plot, being negatively correlated with a plot's slope. Numbers may go down on steeper slopes because of the physical instability of the habitat. Runoff is likely to be swifter and have more energy to shift leaf litter, soil, and stones. As a result, it may be harder for most species to establish themselves and generate large populations.

The ANOVA showed that numbers, richness, and mass were higher and diversity lower on NE plots than on SW plots. A number of factors could account for this result. For the MOFEP sites, annual tree growth is slightly higher on NE stands, 0.61 m^2/ha vs. 0.59 m^2/ha (Jensen 1995), tree basal area is greater, there is more litter cover, and there is less bare soil and rock (Grabner 1995). Because soil moisture is higher on NE stands, microbial and fungal growth must also be higher. With a higher plant productivity, greater and more uniform litter cover and a higher rate of breakdown by microbes and fungi, the NE plots ought to be able to support a larger and richer arthropod community. These results are consistent with those of Mudrick *et al.* (1994) and Seastedt and Crossley who found higher numbers of microarthropods on north-facing forest slopes. Interestingly, the larger arthropod populations of NE plots in our study did not seem to be translated into larger vertebrate populations, at least for reptiles and amphibians. In the same MOFEP sites that were sampled for leaf litter arthropods, reptile and amphibian numbers were consistently lower on NE stands than on SW stands (Renken 1995).

The differences for community characteristics among sites are harder to account for, because the three sites were considered roughly equivalent. One explanation may be the lower pH of soils in site 1. The activity of bacteria and actinomycetes falls rapidly at pH values below 5.5 though fungi function well at all pH levels (Brady 1974). If the lower pH of site 1 caused the decomposer resource base to be reduced to fungi, only those species that specialized on fungi would do well. As a consequence, their numbers would increase relative to species dependent on bacteria and actinomycete food chains, leading to a reduction in the diversity value. There might also be an overall decrease in numbers and richness. What is not clear is why mass did not also decrease. Unfortunately, this explanation of pH effect appears to be contradicted by the fact that SW plots had higher diversities than NE plots even though they had lower pH values.

Two other factors complicate the generalized picture of the leaf litter community. Although there was a significant effect when plot aspect was used, there was little or no effect on numbers, mass, richness, and diversity when stand aspect was used. In other words, the orientation of the plot or local environment was important, but not the orientation of the stand or general environment. This suggests that disturbances would have to be on or near a plot to have much impact, so an activity like logging may have little direct influence on the leaf litter community outside of the area where trees are actually removed. The second factor is the fact that SW-facing plots in this study had significantly steeper slopes than NE-facing plots. Because numbers were negatively correlated with degree of slope, differences between northeast and southwest plots might be due to steepness as well as, or instead of, things like primary plant productivity or fungal growth. These two factors, along with pH, will have to be taken into account when evaluating the impact of the logging treatments.

The Collembola, or springtails, were key species in this community. This group of primitive wingless insects typically forms large populations in the soil and leaf litter. The common name "springtail" comes from the ability of many species to spring out of harm's way using a furcula, a forked, tail-like structure held under the body until the animal is disturbed, when it is then flipped down and back propelling it upward and forward. Collembola are generally fungivorous, though they occasionally engulf leaf litter and even nematodes when they are abundant (Coleman and Crossley 1996). Some species feed selectively on different types of fungi and may thereby affect the speed and direction of forest successions. They are also a significant prey species for a variety of predators (Coleman and Crossley 1996, van Straalen *et al.* 1985) including toads, frogs, and salamanders as well as arthropod predators, like spiders, beetles, and ants.

A preliminary search of the literature uncovered relatively little information on the particular species found at the MOFEP sites, but various species of the genera *Tomocerus* (Takeda 1981) and *Lepidocyrtus* (Seipel 1994) have been described as epigeic, or surface dwellers, on leaf litter. They are characterized by relatively long legs, long antennae, a long furcula, large eyes, a pigmented integument, and in the case of *Lepidocyrtus* species, distinctive dark and light markings. Therefore, our three species, *Tomocerus lamelliferous*, *Tomocerus elongatus*, and *Lepidocyrtus* sp. 149, probably constitute a group of active, surface dwelling Collembola in our community. Three soil dwelling species, *Onychiurus ramosus*, *Folsomia stella* , and *Pseudosinella* sp. 367, were characterized by

reduced legs, antenna, furcula, eyes, and pigmentation. The remainung species, *Hypogastrura brevis*, is an intermediate form, with reduced legs, antenna and furcula like the soil dwelling group, but distinct eyes and pigmentation like the litter surface group. These different kinds of Collembola in one community may be a good indicator of the quality of the leaf litter community. The more active species can exploit small and scattered patches of litter, while the soil species colonize deeper and more continuous layers of litter. Together, they may be more effective at converting the fungi into biomass for animals higher on the food chain.

Only *Onychiurus ramosus* showed a strong difference in its distribution, being more abundant on NE plots. An important factor might be that the litter appears to be distributed more uniformly on NE stands (Grabner 1995). *Onychiurus ramosus* in particular is poorly adapted to cross open spaces, so it may be able to build larger populations where the litter cover is relatively continuous. *Folsomia stella*, another deep litter species, and *Lepidocyrtus* sp. 149, a surface litter species, were also more abundant on NE plots or stands. *Folsomia stella* may be more abundant on NE plots for the same reason *Onychiurus ramosus* is, but it is not clear why *Lepidocyrtus* should show a preference. If the different cutting treatments affect the distribution and depth of leaf litter significantly, there may be a shift in dominance among deep litter and surface litter species.

The Oribatid mite in the family Euphthiricaridae also preferred NE plots. It is a specialist on downed dead wood, and because of the higher plant productivity on NE stands, there is likely to be more woody material. However, it is not likely to respond rapidly to changes in availability of its resource. In general, the Oribatid mites are slow growing, slowly reproducing K-selected species (Coleman and Crossley 1996), so it might take years for an environmental disturbance to shift their population numbers significantly.

Because forest food webs may have many links, they may be buffered against changes in the prey populations. Therefore, dominant generalist predators may not be very good indicators of environmental change. Both the Mesostigmatid mite and the Pseudoscorpion probably feed on anything they can overpower, so their numbers may not fluctuate much even with significant changes in the arthropod community. The Pseudoscorpion, a miniature scorpion-shaped arachnid without the tail, was somewhat more abundant on NE plots. It may be able to respond more rapidly to changes in numbers or mass than the Mesostigmatid mite, or it may be specialized on species that do better on NE plots.

CONCLUSIONS

There were 22 orders of arthropods and 547 morpho-species in the leaf litter samples collected from MOFEP sites 1, 2, and 3. In terms of numbers, mass, and richness, the community was dominated by Diptera (adults and larvae, mostly Cecidomyidae), Coleoptera (adults and larvae), Araanea (mostly Gnaphosid spiders), and Acari (oribatid, mesostigmatid and prostigmatid mites). The numbers, mass, and richness of arthropod leaf litter communities were significantly higher on NE- than on SW-facing plots, while diversity (inverse Simpson's index) was significantly lower. There were also differences among the forest sites we sampled, but only strongly for diversity. Because some of the physical features of the plots varied with plot aspect (NE plots had less steep slopes and higher pH than SW plots) and with site (site 1 had a lower pH than sites 2 and 3), aspect and site effects may be confounded by slope and pH. When stand aspect was used instead of plot aspect, differences for numbers, mass, and richness became weaker or disappeared, which suggests that local (as in arthopod sampling plot) conditions may be more important in shaping leaf litter communities than general (as in stand) conditions. Of the 547 morpho-species identified, 10 contained 47 percent of the individuals found. Seven of these were Collembola, primitive, wingless insects specialized on fungi. These could be sorted into the active surface-dwelling species capable of traversing open spaces between patches of litter, and the less mobile soil/humus-dwelling species limited to deeper and more extensive litter patches. The other dominants included a mite specialist on woody material (Euphthiricaridae), and a mesostigmatid mite and a pseuodoscorpion (both predatory). Three of the Collembola, the Euphthiricarid mite, and the Pseudoscorpion were either somewhat or significantly more numerous on NE plots.

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