

Trophic Level Effects on Species Diversity in Arthropod Communities of Forest Canopies¹

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ABSTRACT

Species diversity for arthropod communities inhabiting white pine and coppice canopies was measured using the Shannon Wiener information theory index, $H(s)$, the Margalef index, D , and the Pielou evenness index, J' . The 2 insect orders Coleoptera and Hymenoptera were investigated. The general index $H(s)$ was significantly higher for the more diverse coppice stand than for the white pine monoculture, and was significantly higher for Hymenoptera than for Coleoptera. The other 2 indices demonstrated that differences in diversity between watersheds were due to greater species richness in the coppice, while differences between insect orders were due to greater evenness of individuals in the Hymenoptera. Since the Coleoptera were principally herbivores and the Hymenoptera predator-parasites, results can be interpreted in a trophic level context. It is suggested that, in a plant monoculture, low diversity is not propagated along food chains but rather is recovered at higher trophic levels.

Arthropod communities of forest canopies are among the least known entities of forests. Studies of forest insects usually concern pest species and are conducted at the population level. For the most part, these studies have concentrated on outbreak situations, with little attention given to arthropod populations at low, pre-outbreak levels. Research now being conducted as part of the Eastern Deciduous Forest Biome program of the US/IBP is attempting to quantify mineral element dynamics for communities of canopy arthropods. Evidently, canopy arthropods process a small part of the energy and mineral elements accumulated by trees during leaf production (Reichle and Crossley 1967), but such measurements do not describe adequately the role of canopy arthropods in forests. Management or manipulation of forested watersheds may alter the canopy-arthropod community so as to increase the potential for pest outbreaks or disease transmission. Forest management plans now include the maintenance of a diverse community of arthropod predators and parasites as a goal that is desirable, if difficult to attain.

Various measures of species diversity continue to be useful means of describing community organization, as well as quantifying changes occurring naturally or induced by manipulation (Woodwell and Smith 1969). In the present paper we report some indices of diversity for Hymenoptera in 2 manipulated watersheds, and compare these data with previously published results (Coulson et al. 1971) for Coleoptera in these watersheds. In these canopies the majority of the Hymenoptera are parasites or predators, so that comparisons of trophic levels can be made. Regrettably, samples could not be taken in adjacent control (unmanipulated) watersheds, because of the difficulty of getting into those higher

canopies. The 2 watersheds sampled had canopies which were readily accessible.

The purposes of this study involved a comparison of species diversity for canopy-insect communities in 2 manipulated watersheds: a white pine (*Pinus strobus* L.) plantation and a coppice (mixed hardwoods regenerated from stump growth). We assumed a priori that the coppice community would contain more insect species because plant diversity was much greater. We could not assume that apportionment of individuals among species would be reduced or increased, a hypothesis testable with several indices of diversity. Secondly, by comparing herbivore and predator diversity we hoped to discover whether the ends of food chains would magnify species diversity or reduce it. The other purposes were methodological, and concerned the validity of trapping only flying adult insects with the particular methods we used. Results showed that behavioral traps were indeed adequate in watersheds of this size (13–16 ha). One of the trapping methods (sticky boards) proved inadequate; of the other 2, malaise traps were less effective than window-flight traps, but both were useful.

Materials and Methods

The experimental watersheds sampled are in the Coweeta Hydrologic Laboratory, Macon County, NC. Major features and history of that laboratory are given by Johnson and Swank (1973). Watershed 13 was a 16-ha, 7-year-old hardwood coppice at the time of sampling (1969). Twice (once in 1939, and again in 1962), all woody vegetation on the watershed was cut and left in place. In 1969 the coppice consisted of a regrowth of hardwood species, with *Quercus* spp., *Carya* spp., *Liriodendron tulipifera* L., and *Cornus florida* L. accounting for 70% of total basal area. Watershed 17 is a 13-ha white pine (*Pinus strobus* L.) plantation established in 1956. In 1969 it averaged 15.3 m²/ha basal area (Johnson and Swank 1973). For sampling insects, platforms were constructed in the middle canopies of both

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watersheds. Three trapping methods were utilized: malaise traps, 1-ft² sticky traps, and window-flight traps. Best results were obtained with the window-flight traps (described in Coulson et al. 1970). Sticky-trap collections were finally abandoned, and data discussed below are based on lumped collections from the malaise and window flight traps. Samples were taken at weekly intervals from July 4 to October 28, 1969, a total of 11 samples. Insects were identified to family, and sorted to species types.

Three indices were calculated to measure aspects of species diversity: The Shannon-Wiener function $H(s)$ is given by:

$$H(s) = - \sum_{r=1}^s Pr \log Pr$$

where s is the total number of species in a sample and Pr is the observed proportion of individuals belonging to the r th species ($r = 1, 2, \dots, s$). The Margalef index D is given by:

$$D = (s - 1) / \log_e N$$

where N is the total number of species in the sample (Margalef 1957).

The apportionment of individuals within species was measured with the evenness index J' (Pielou 1966):

$$J' = H(s) / H(s)_{\max}$$

where $H(s)$ is the observed diversity and $H(s)_{\max}$ is the maximum possible diversity for the sample. $H(s)_{\max}$ is numerically equal to $\log_e s$.

Results and Discussion

The insect communities in white pine and coppice canopies differed measurably. Predictably, the coppice canopy supported a larger number of species types than the white pine canopy for both the Hymenoptera and Coleoptera (Table 1). Mean numbers of species per sample and individuals per sample were higher in the coppice watershed than in the white pine watershed. Graphic methods (Sokal and Rohlf 1973) indicated that, for Coleoptera, the distribution of individuals per sample was strongly skewed to the right. The distribution of individuals per sample for Hymenoptera was normal, as was the distribution of species per sample for both orders.

Surprisingly, more species of Hymenoptera than Coleoptera were collected in the White Pine watershed. Also, mean species of Hymenoptera per sample exceeded mean species of Coleoptera in the white pine watershed (Table 1), although the difference is not statistically significant. Individuals of Coleoptera outnumbered the Hymenoptera. Doubtless, trapping efficiencies were different for 2 orders. Malaise traps are relatively less efficient for Coleoptera compared to Hymenoptera (Matthews and Matthews 1971), but window-pane traps do collect Coleoptera efficiently (Coulson et al. 1970). Our calculations are based on lumped data from the 2 kinds of traps. Also, we would expect similar efficiencies in the 2 types of watersheds.

Table 2 summarizes the 3 indices of diversity calculated for the samples of insects. Each was examined with a 2×2 analysis of variance to detect differences between means for the 2 watersheds and the 2 insect orders. Index $H(s)$ is the more general 1 of the 3, in that it responds to both species richness and evenness of distribution of individuals among species. For $H(s)$, significant differences could be shown for both watersheds and insect orders ($P < 0.01$). The index J' is primarily a measure of evenness of distribution of individuals among species. For J' , differences between means for the insect orders were significant ($P < 0.05$), the index being higher for Hymenoptera than for Coleoptera, but differences between the 2 watersheds were nonsignificant. For the index D , a measure of species richness, differences between means for watersheds were significant ($P < 0.01$), the coppice being higher, but differences between means for the insect orders were not significant. In summary, the generalized index $H(s)$ detected differences between watersheds and between insect orders, the former probably due to greater species richness in the coppice (Index D) and the latter due to greater evenness in allocation of individuals per species in the Hymenoptera (Index J').

Lumping the 2 insect orders together to simulate an entire community yielded large values for Index D . For the coppice, the mean was 12.9 (± 1.40), for the white pine watershed, 5.1 (± 0.40); the difference between means was statistically significant ($P < 0.01$). This index is sensitive to sample

Table 1.—Numbers of individuals and species of 2 insect orders collected in coppice and white pine watersheds, Coweeta Hydrologic Station, NC. Based on 11 samples/each watershed, using malaise traps and window flight traps, July 9–September 27, 1969.

	Coppice			White Pine		
	Total species	Species/sample (mean) ^a	Individuals/sample (mean) ^a	Total species	Species/sample (mean) ^a	Individuals/sample (mean) ^a
Coleoptera	165	42.0 ± 9.0	395 ± 137	35	8.5 ± 1.5	58 ± 20
Hymenoptera	107	36.6 ± 4.4	91 ± 16	43	12.8 ± 1.8	24 ± 5
Coleoptera + Hymenoptera	272	78.7 ± 12.5	486 ± 148	78	21.3 ± 2.4	82 ± 18

^a Mean ± SE.

Table 2.—Mean values and standard errors for indices of species diversity for the insect orders Coleoptera and Hymenoptera, collected in canopies of a White Pine and a coppice watershed, Coweeta Hydrologic Station, NC, summer, 1969. Means based on 11 samples. H(s), J' and D explained in text.

Index	Watersheds			
	Coppice		White pine	
	Coleoptera	Hymenoptera	Coleoptera	Hymenoptera
H(s)	2.455 ±.117	3.009 ±.021	1.710 ±.119	2.275 ±.151
J'	.720 ±.036	.848 ±.037	.783 ±.047	.881 ±.036
D	7.15 ±1.01	7.94 ±.782	2.38 ±.237	4.13 ±.401

size, so that lumped values for insect orders exceeded the individual values. The evenness index J' for lumped samples of Coleoptera and Hymenoptera was intermediate between the 2 values for the orders. Differences between means for the 2 watersheds were not significant. Means were 0.723 (± 0.039) for the coppice and 0.773 (± 0.049) for the white pine watershed. The general index H(s) for lumped insect orders was slightly higher than the individual values. Differences between means for the watersheds were statistically significant ($P < 0.01$). Means were 3.024 (± 0.147) for the coppice and 2.355 (± 0.159) for the white pine watershed.

There is little published information on diversity in terrestrial arthropod communities which can be interpreted on a trophic level basis. The range of values reported here for the 3 indices is quite similar to that found by Barrett (1968) in an experimental grain field (data recalculated by Odum 1971). For the general index H(s), little difference was found between trophic levels by Barrett. In our study the Hymenoptera, considered to represent predators, were slightly more diverse than the Coleoptera, considered to be herbivores. The evenness index J' was found to be higher for predators, which agrees with the data of Barrett. Index D evidently is sensitive to sample size, making comparisons difficult, but the index provided distinct information in our study and in Barrett's. The major difference between the 2 watersheds was the richness component, well illustrated by this index. Index D was slightly higher for Hymenoptera (predators). Janzen and Schoener (1968) also described differences in species richness for adjacent (tropical) habitats, in that case influenced by moisture regimes.

These results suggest that changes in diversity are not much propagated through food chains. We did not attempt to measure diversity indices for vegetation but the differences between the 2 watersheds were obvious. For the monoculture pine plantation, herbivore diversity was lowered but predator diversity nearly equalled that of the coppice watershed. Index D showed reduction in species richness most clearly, but was affected by sample size. The other indices indicate a near recovery of species diversity at the predator trophic level. This interpretation as-

sumes that flying adult insects constitute a valid sample of species and numbers, and that the 2 insect orders are models for entire trophic levels. Our data do not include important herbivores (Homoptera and Lepidoptera) or important predators (Araneae) in these canopies. Also, the samples were replicated only through time. Index D decreased significantly through time in samples from the coppice watershed; the other indices did not change significantly with time.

Entomologists often assume that the diversity of insect communities is a direct function of the diversity of their food plants (Ehrlich and Raven 1964). Our results suggest that interactions between trophic levels are important as well, certainly affecting the allocation of individuals within species if not richness itself. Low diversity does not appear to be propagated through food chains, but rather, a significant fraction of diversity is recovered at the highest trophic levels. If the major source of population control for herbivores is predation and parasitism, as has been assumed (Hairston et al. 1960), then such control should exist, at least potentially, in the white pine monoculture. On that basis, a monoculture of plant species may not be inherently more susceptible to outbreaks of insect herbivores, than is a more diverse plant community. However, the number of competitive or trophic interactions between species may be more significant to community stability than is species diversity alone.

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