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The Influence of Variation in Litter Habitats on Spider Communities

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Summary. Spider communities were sampled over an artificial gradient of litter depth (created by raking) and compared to those of two other forests exhibiting natural variation in litter depth. More species of spiders were present in areas of greater depth and/or complexity in all sites. Relative abundance of Lycosidae decreased, while relative abundance of Clubionidae, Thomisidae and Gnaphosidae increased over gradients of increasing depth and complexity. Similarity of species composition between areas within a forest was related to site differences in litter depth and structure.

As litter depth increased, there were significant changes in prey species richness, litter complexity, and microclimate. Partial correlation analysis of grouped data from early-, mid-, and late season suggests that influential factors change with season. In the early season, prey abundance and temperature variation account for most of the variation in spider species richness. In mid-season, litter complexity and moisture fluctuations appear to influence richness, with complexity relatively more important. In late season, complexity and temperature range were the primary factors, with temperature relatively more influential. The relative importance of these factors in influencing community structure of spiders is discussed.

Introduction

The spider fauna of leaf litter may be divided into various guilds (Root, 1973) based on methods of prey capture and utilization of similar prey resources. One guild, the wandering spiders, may constitute upwards of 43% of ground dwelling spider species in a forest (Drew, 1967), and accounts for a majority of the biomass of spiders (Moulder and Reichle, 1972). These spiders do not use webs in prey capture, but use a "sit-and-wait" foraging strategy, with frequent changes of site (Ford, 1977; Edgar, 1969). Their prey consists mainly of Collembola, Homoptera and small Diptera (Breymeyer, 1966; Edgar, 1969; Moulder and Reichle, 1972). The wandering spider guild includes the families

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Clubionidae, Gnaphosidae, Lycosidae, and Pisauridae, Thomisidae, and some representatives of the Agelenidae and Hahniidae. Enders (1976) has suggested that this group be subdivided into numerous guilds, based on reproductive characteristics and presumed differences in foraging speed. Data on foraging strategies in most spiders are scarce or non-existent, and at this time it is difficult to separate them beyond the original designation of wandering, jumping and web-spinning spiders, as suggested by Balogh and Loksa (1948).

Previous studies have demonstrated that differences in litter type (mull vs mor; maple-beech vs oak) are accompanied by differences in the composition of the spider fauna (Lowrie, 1948; Berry, 1967; Jocque, 1973). Hagstrum (1970) found that litter depth affects spider abundance, with the greatest numbers of individuals occurring in the deeper litter.

In studies of two temperate deciduous forests (Illinois and Delaware), I observed that spider diversity and species richness were correlated with depth and interstitial volume of litter. In this study, I created an artificial gradient of litter depth in an Illinois forest and sampled it periodically for changes in number of species and individuals. The results were compared with those of two other pitfall studies in forests exhibiting natural variation in litter depth (Uetz, 1975, 1976). Changes in species richness and composition were related to variation in aspects of the litter environment likely to change with litter depth (prey abundance, diversity, microclimate, etc.). The guild of cursorial spiders was chosen for this study because of their dominance in forest litter microcommunities over a wide range of habitat types (bare soil to complex litter) and because their wandering habit implies independence from use of habitat structures in prey capture (i.e., web site architecture).

Methods

This research involves 3 studies, separated in space and time, but similar in methodology. Wandering spiders were collected by pitfall trapping over an artificial gradient of litter depth in an Illinois forest, and in 2 other forests (one in Illinois and one in Delaware) exhibiting a wide range of variation in litter depth. The Delaware forest is an Oak-Tuliptree-Maple forest, located on the University of Delaware Agricultural Experiment Station Farm in Newark, Delaware. The forest is mesophytic, and is on level to gently rolling topography. Litter variation in the Delaware woodlot was primarily due to varied species composition and leaf structure in each site. More detailed information on this study area is available in Uetz (1975).

One Illinois field study took place in a streamside forest at Robert Allerton Park near Monticello, Illinois, on the Sangamon River. The study area consists of ca. 1.6 hectares of shallowly sloping flood plain and gradually rising topography. The elevational gradient from the river bank to the uplands provides a continuous forest gradient over decreasing annual flood frequencies (25% at bank level to 0% in the uplands). Forest composition, litter depth and litter structure are all affected by the frequency and duration of flooding at each level. Flood plain areas are dominated by silver maple, while upland areas are dominated by white and black oak. A transition zone exists between them, with representative species from each area, in addition to shingle oak and hackberry. Further information on the study area can be found in Uetz (1976).

The Hart Memorial Woods, owned by the University of Illinois, located along the East bank of the Sangamon River near Mahomet, in Champaign County, Illinois, was the site of the experimental litter study. A recent survey (Root et al., 1971) describes the upland area as somewhat xerophytic, covered by a mixed stand of *Quercus alba* L. (white oak), *Q. velutina* Lau. (Black oak), and *Q* *rubra* L. (red oak). Further information on vegetation and soils can be found in Root et al. (1971), and Bell and Sipp (1974).

A 50 × 100 m plot on level topography dominated by white oak was chosen for experimental manipulation of litter. The site was covered with a continuous litter of homogeneous structure. Litter depth averaged 3–4 cm, leaves were mostly of the curled or bent type (Heatwole 1961), and humus was less than 1 cm deep. The 50 × 100 m plot was subdivided into 50 10 × 10 m squares, from which 15 experimental plots (100 m^2) were chosen. Prior to experimental manipulation, I measured several aspects of the litter environment. As described in Uetz (1974), I took ten measurements of litter depth, litter species composition, and interstitial volume in each plot. Soil moisture was determined gravimetrically in each plot on 3 successive days. Soil surface temperature ranges were recorded with maximum-minimum thermometers over a period of one week (prior to trapping). Litter energy content was estimated using data on litter species composition and biomass/m^2 from the study site, and calorific measurements of litter from a similar forest downstream on the Sangamon River (Bell and Sipp, 1975). Analysis of variance for each of these parameters showed no significant differences between plots.

The 15 experimental plots were arranged as 3 replicates of oppositely-directed, 5-step gradients of litter depth, with a pitfall trap located in the center of each plot. Plots were separated from each other by one plot in all directions within a matrix of natural litter. Litter depth in the plots was altered by raking to approximate multiples (0, 0.5, 1.0, 1.5, 2.0) of a mean depth obtained from pooled data from all plots, 3.345 ± 0.111 cm (± 2 SE). Litter removed from the "0" plots was distributed over the 2 × plots, while $^1/_2$ the litter from the ".5" plots were placed in the 1.5 × plots. All plots, including controls, were disturbed equally by raking.

The plots were raked in early March and allowed to stabilize for a period of 3 weeks. During this period a 4-inch snowfall occurred, compressing the loosely distributed leaves (23 Mar). After the stabilization period, and twice during trapping, measurements of the previously mentioned variables were taken again (except for temperature, which was monitored on a weekly basis). While litter plots within each series showed significant differences, no significant differences were found between replicates. Replicate depths were within 1 S.E. of the desired depth. Preparation of the area was completed in mid-March. It was felt that the litter at this time did not support a large population of active wandering spiders, (spiderlings had not emerged from egg sacs, and immatures were still overwintering in logs) and that the impact of raking and litter removal would be slight.

Comparison of methods has shown pitfall trapping to provide the closest estimate of the number of species in a community (Uetz and Unzicker, 1976). In addition, it permits continuous sampling of temporally stratified species. In both the Illinois studies, the trap was made from an institutional food can (15 cm diameter; 22 cm depth) with a 10 cm metal collar soldered to the rim (Uetz and Unzicker, 1976). Inside the can a plastic funnel (same diameter as the can) lead to a plastic jar (10 cm diameter; 7 cm depth) containing ethylene glycol preservative. In the Delaware study, a smaller trap made entirely of plastic was used (see Uetz 1975 for details). The pitfall traps were buried flush with the soil surface. Contents were collected on a weekly basis from June–September 1970 in the Delaware study, and from April–October 1973 in both Illinois studies. In the experimental litter study, traps were opened for a week at a time every other week. It was hoped that this trapping schedule would not seriously deplete local populations, yet would provide information on temporally segregated species. Number of species, number of individuals of each species, and numbers of individuals in families were known for each study area. Each study had approximately the same number of sample points representing pitfall trap collections: 15 plots of altered litter depth; 15 locations in the Delaware woods; and 13 elevations over the Allerton flooding gradient. In each case, minimum sample sizes were arrived at by species/sample size curves and S.E./ratios, as described in Uetz and Unzicker (1976). In each study, collections were made on the same day over a period of <1 h, and all traps were open for the same periods of time. Additional data from each of the study areas on aspects of the litter environment were available from my own measurements or from previous studies. Estimates of prey species richness were made from pitfall trap collections and quadrat sampling of other arthropods at each site.

It is obvious that intercorrelation of independent variables is likely to be a problem when considering the influence of the complex set of environmental factors affecting spider diversity. It is impossible to control for all variables in a field experiment, especially those so closely related to litter depth. Choice of a site with homogeneous litter structure was expected to control for differences in litter complexity, but it became obvious that the various litter treatments would behave differently with regard to litter compaction over the season. Deeper litters tended to maintain complexity after snowfall and rain, while shallower litters tended to compress more easily. Thus, a statistical method capable of holding one or more variables constant while testing the influence of another is indicated in situations where all variables cannot be held constant experimentally. Partial and multiple partial correlation (Blalock, 1972) met those requirements. From the behavior of partial correlation coefficients, we may uncover spurious relationships and infer a hierarchy of (relative) influence among variables.

Results and Discussion

Data from pitfall trap collections over gradients of litter depth in two geographically separate forest areas and in the Illinois experimental plots indicate that variation in litter habitat affects spider diversity. Correlations between species richness and litter depth were significant in all areas (Hart $r=0.851$, $p<0.005$; Delaware $r=0.760$, $p<0.005$; Allerton $r=0.945$, $p<0.005$). Moreover, the regression lines (fitted by least squares) for these relationships were very similar in slope (Fig. 1). The regression line for the relationship between litter depth and species richness at Allerton Park has a steeper slope than the others, possibly because areas with lower litter depth occur in the flood plain (where flooding not only depresses litter depth but limits distribution of some species).

It is interesting that a similar relationship exists between the depth of litter and the existing number of spider species in both natural and artifically manipulated litter habitats, and in forests that differ in species composition and geographical location. Stanton (pers. comm.) found species richness of leaf litter mites to be the same in comparable temperate and tropical habitats with standardized amounts of litter resources. From these results, she concludes that the number of coexisting species per sample is regulated by the amount of litter present. Several previous studies have found increased spider abundance with increased litter depth (Lowrie, 1948; Hagstrum, 1970; Berry, 1967), but species richness has not been mentioned. The litter habitat may affect spider species richness by providing prey, reducing temperature fluctuations, maintaining moisture, providing structural retreats, and introducing a heterogeneous substrate for refuging from predation. The relative importance of these variables will be discussed in a later part of this paper.

Examination of differences and similarities in spider species composition over gradients of litter habitats, or between areas with different litter types may provide insight into the influence of litter variation on spider communities.

A total of 578 specimens was collected from the experimental litter plots; representing 6 families, 12 genera, and 21 species of wandering spiders (Table 1). (Data on species collected in the other studies are published in Uetz, 1975, 1976). These totals are lower than for the Delaware and Allerton Park studies, which collected 33 and 26 *sp.*, respectively. The total number of species collected in each plot was used as an estimate of species richness, and these data were subjected to testing by analysis of variance. Since no significant differences in environmental variables were found between replicate plots of equal depth prior to the experiment, the three experimental gradients may be treated as

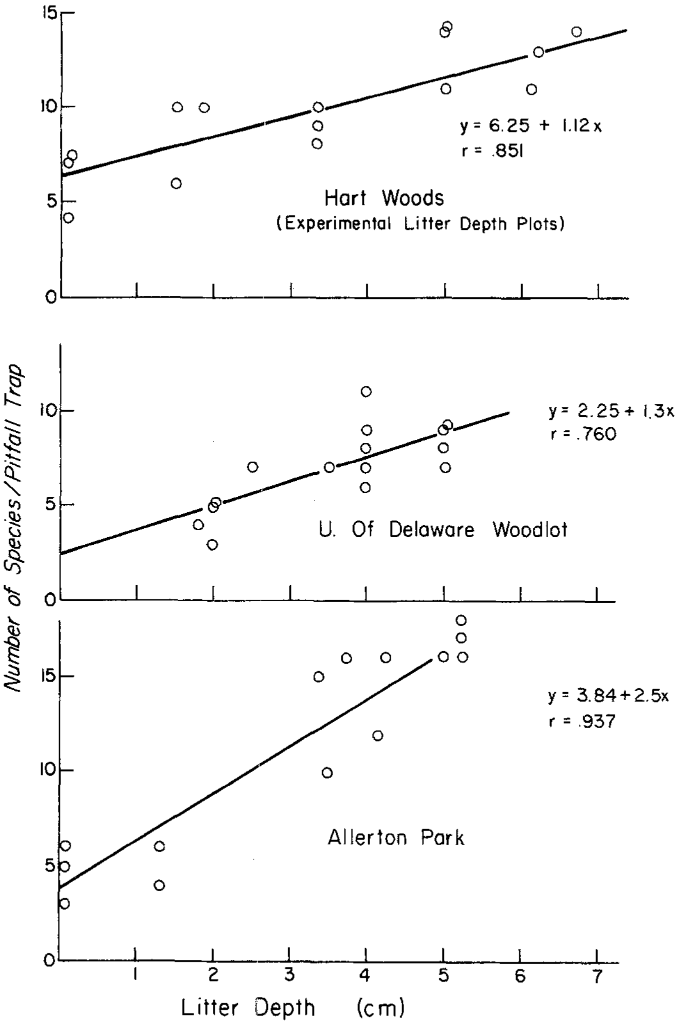

Fig. 1. Comparison of regression lines for the relationship between litter depth and number of spider species per pitfall trap in the three study areas

random effects. The litter treatments for each plot within a gradient must be considered a fixed treatment, allowing a mixed-model two-way analysis of variance to be used (Sokal and Rohlf, 1969). Results of the ANOVA show no significant differences in species richness between replicate plots, and highly significant differences ($F = 16.31$, $p < 0.001$) between litter treatments. From the fixed treatment design, it is possible to conclude that highly significant increases in spider species richness occur as litter depth increases. The same ANOVA method was used to test numbers of individuals collected and several environmental variables mentioned previously (Table 2). No significant differences in numbers were found, either between replicates or between treatments for soil

Table 1. Abundance of wandering spiders collected from pitfall traps in plots in the experimental litter study in Hart Memorial Woods, April–September 1974

Species	No litter	$^{1}/_{2}$ litter removed	Natural litter depth	$1^{1}/_{2}\times$ natural depth	$2\times$ natural depth
Family Agelenidae					
Cicurina robusta Simon	5	4	2	2	3
Family Clubionidae					
Castaneira cingulata (Koch)	0	1	0	4	0
C. longipalpus (Hentz)	1	2	0	8	12
Meioneta sp.	0	0	1	0	0
Phrurotimpus alarius (Hentz)	1	12	10	11	9
P. borealis (Emerton)	1	3	6	2	4
No. of species	3	4	3	4	3
Family Gnaphosidae					
Drassyllus aprilinus (Banks)	0	0	0	1	0
D. fallens Chamberlin	2	0	1	1	1
D. niger Chamberlin	0	3	7	8	4
D. virginianus Chamberlin	1	3	1	5	2
Sergiolus sp.	0	0	0	0	1
Zelotes sp.	0	0	0	1	2
No. of species	2	2	3	5	5
Family Hahniidae					
Hahnia cineria Emerton	0	0	0	1	0
Family Lycosidae					
Lycosa gulosa (Walckenaer)	0	0	0	3	2
Pirata minuta Emerton	57	55	62	41	50
Pirata sp.	11	12	3	37	11
Schizocosa saltatrix (Hentz)	2	1	2	7	2
S. rovneri Uetz & Dondale	5	13	3	6	7
No. of species	4	4	4	5	5
Family Thomisidae					
Xysticus elegans Keyserling	0	0	2	4	2
X. ferox (Hentz)	0	1	1	2	3
X. fraternus Banks	2	3	2	8	10
No. of species	1	2	3	3	3
Number of species	11	13	14	19	17
Number of individuals	88	113	103	152	125

Table 2. Mean values (±2 S.E.) for several variables measured as part of the experimental litter study in Hart Memorial Forest. (Litter variables – depth, interstitial space, energy content – are initial values; all others are seasonal means.)

Variable	No litter	$^1/_2$ litter removed	Natural litter depth	$1^1/_2\times$ natural depth	$2\times$ natural depth
Litter depth (cm)[a]	0.0	1.59 ±0.20	3.28 ±0.05	4.87 ±0.09	6.33 ±0.35
Interstitial space[a] (cm^3/cm^2)	0.0	1.15 ±0.10	2.20 ±0.06	3.31 ±0.06	4.30 ±0.24
Litter energy content[a] ($Kcal/m^2$)	0.0	1,381.6 ±98.8	3,006.1 ±59.7	4,226.7 ±131.8	5,678.3 ±421.9
Soil moisture (%)	0.28 ±0.02	0.31 ±0.02	0.29 ±0.03	0.30 ±0.01	0.30 ±0.03
Soil temperature range[a] (max-min)	22.1 ±2.6	23.2 ±2.3	16.4 ±2.3	18.0 ±1.4	15.0 ±2.0
Prey abundance (no./trap week)	16.6 ±19.3	34.3 ±24.7	28.7 ±15.5	45.0 ±21.2	45.3 ±45.9
Prey species richness[a]	10.0 ±5.0	15.3 ±4.8	15.0 ±2.3	16.0 ±2.0	17.0 ±4.0

[a] Differences between experimental treatments are significant ($p < 0.05$)

moisture, prey abundance or spider abundance. Significant increases in prey species richness ($p < 0.05$) also occur as litter depth increases.

Changes in community composition at the family level over the gradient of litter in the Hart plots show a pattern similar to those found in earlier studies (Fig. 2). There is a gradual decrease in the dominance of Lycosidae, with a consequent increase in the dominance of three other families – the Clubionidae, Gnaphosidae and Thomisidae – with increased litter depth (differences are significant at $p < 0.001$; G-test). Although there is little change in the number of families represented over the gradient, there are significant increases in the number of species within two families: the Gnaphosidae (2–5) and the Thomisidae (1–3) (Table 1).

These results substantiate earlier notions about the influence of litter structure on spider communities. Removal of litter from plots resulted in increased dominance of the Lycosidae. In the Allerton study, lycosids predominated in areas where litter was removed or greatly compressed by flooding. Similar results were found in the Delaware study in part of the forest dominated by swamp chestnut-oak. The litter in this area is shallow and compressed due to leaf type and to water accumulation. Change in the litter habitat from a three-dimensional substrate to a flat surface may give wolf spiders a competitive advantage, or make other spiders subject to predation by them. Addition of litter is accompanied by increased dominance of litter-dwelling spider families that live within the litter (Gnaphosidae, Clubionidae, Thomisidae). Several of the species added with increased litter in this study are mentioned in the literature

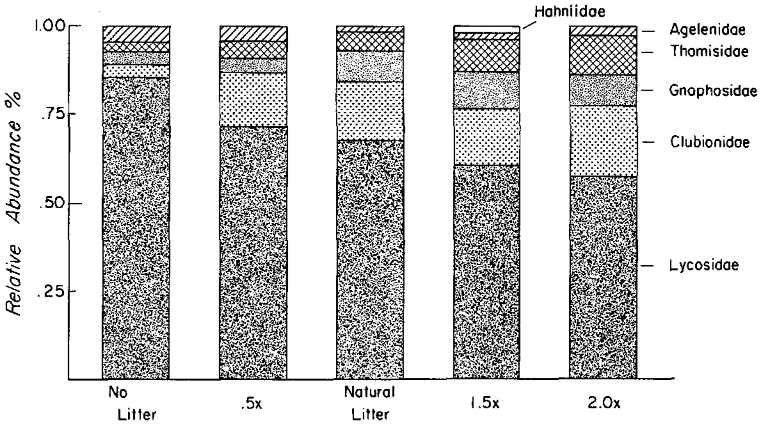

Fig. 2. Relative abundance of spider families in the treatment groups of the artificial litter depth gradient at Hart Woods

as building silken retreats and egg cases in rolled leaves. Huhta (1971) and Lowrie (1948) found similar increases in "within-litter" spider families in forest succession, where litter accumulation over time changes the nature of the forest floor from a flat surface to a three-dimensional substrate. Deeper litter undoubtedly provides increased habitat resources for such species and possibly improves their survivorship. These data all suggest that more families (and species) are added to the community as litter becomes deeper and/or more complex because of the greater variety of microhabitats and prey items provided, or possibly because heterogeneity reduces interspecific predation (allowing rare species to persist).

Indices of similarity in species composition were calculated for all possible pairs of experimental plots (Sorenson 1948). There is a significant negative correlation between the degree of similarity of two plots and the difference in litter depth between them (Spearman rank correlation: $r = 0.707$, $p < 0.005$). The inverse relationship observed here suggests that groups of species may be associated with litter of a certain depth or structure, as noted in both the Delaware and Allerton Park studies. These findings offer further support for the hypothesis that variation in litter habitats influences the structure and composition of spider communities.

Further evidence of the influence of modification of the litter habitat on spider communities has been found in cluster analysis of species composition at elevational sites along the flooding gradient at Allerton Park (Uetz, 1976). The cluster analysis showed major decrease in similarity ($\simeq 80\%$) between sites above and below the upper limit of compressed litter/lower limit of complex upland litter. Other breaks between similarity clusters demarcate natural divisions in the physical structure of litter on the flood plain-uplands gradient. Upland areas have a high degree of between-site similarity.

The data examined here suggest that differences in the physical structure of leaf litter influence species composition. Duffey (1966) has suggested that habitat structure plays an important role in limiting the distribution of some spider species. Barnes and Barnes (1955) and Luczak (1963) have shown that spider communities exhibit a high degree of constancy in structure and composition in widely separated plant communities of a specific type (e.g., broomsedge field, pine forest). They suggest that there is a relationship between the structure of plant communities and the communities of spiders that inhabit them. Jocque (1973) has demonstrated that adjacent forests with contrasting litter types have only 40.4% similarity in spider species composition and vary significantly with respect to diversity, findings which he attributes to differences in the structure of litter and humus (MacArthur and MacArthur, 1961).

This study included measurement of changes in several environmental variables with altered litter depth, such as litter complexity (interstitial space/volume), litter energy content, litter microclimates (temperature and moisture) and prey resources (abundance and diversity), all of which might influence spider species richness. When data are examined from seasonal totals, partial correlation analysis reveals that litter complexity (interstitial space/volume) and prey diversity account for a majority of the variation in species richness (Fig. 3). Coefficients for other potentially influential variables (i.e., microclimatic factors, prey abundance and litter energy content) were considerably diminished. Interstitial space/volume would appear to be the most influential variable of the two, since the coefficient is much larger. There are many reasons why (an estimate of) litter complexity could be the primary factor influencing the structure of spider communities, and they have been discussed in a previous paragraph, and in Uetz (1975). However, there are also reasons to suspect that such a conclusion might be a result of the manner in which the data were treated. Kulesza (pers. comm.) found that the relationship between bird species diversity and foliage height diversity (MacArthur and MacArthur, 1961) changes in grasslands with seasonal variation in vegetation structure, and at some times of the year may not exist. When these data are examined from seasonal totals, the relationship appears as expected. Spider species richness, when examined as the seasonal total of species from all collections at a site is most likely to be correlated with factors exhibiting little seasonal variation or proportionate change over time, i.e., litter complexity. Other factors (temperature, prey abundance) that rise and fall over the season will be obscured as mean values, while diversity appears as an additive function. Correction of these inequalities by calculating a mean number of species, or expressing temperature as degree-days, is difficult owing to missing data points. However, it is possible to examine spider species richness in space and time simultaneously (Fig. 4) and to see if different patterns arise.

Partial correlation analysis of grouped data from early, mid, and late season suggest that factors influencing species richness over the litter depth gradient change with season. In the early part of the season, prey abundance appears as a factor of primary importance. In this analysis, partial correlation coefficients were calculated using Kendall's tau coefficients (Blalock, 1972), because division of the data by season reduces sample size, and a non-parametric test is appropriate. Unfortunately, these may not be tested for statistical significance. Inferring a path of influence from the magnitude of partial correlation coefficients (Fig.

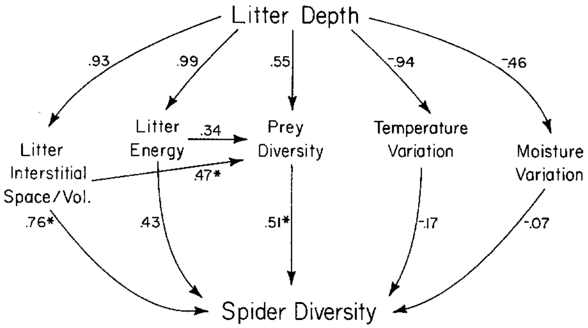

Fig. 3. Partial correlation analysis of variables associated with litter depth and spider species richness, based on season total. Upper row of numbers are initial correlation coefficients (Pearson product-moment) (all significant). Lower row(s) are partial and multiple-partial coefficients. Asterisk indicates significance by F-test at $p = 0.05$

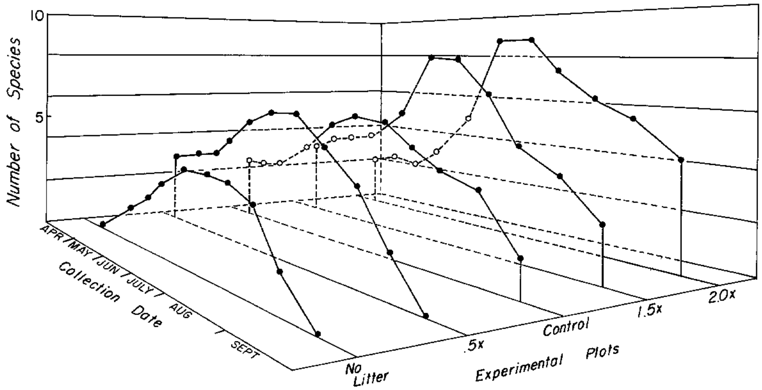

Fig. 4. Comparison of seasonal patterns in spider species richness in the treatment groups of the artificial litter depth gradient at Hart Woods. Each point represents a pitfall trap collection at a site on the gradient at a point in time

5), we might speculate that plots with deeper litter have more abundant prey because microclimatic temperature variation is reduced. Gill (1969) found that non-nutritive, experimental litter (dacron) had abundance levels of soil microarthropods similar to natural litter. Plots with litter removed had greatly reduced abundance. The results demonstrated that moderation of the physical environment by litter was a factor of major importance in determining abundance of soil microarthropods. Prey abundance or activity (and thus effective abundance) accounts for more of the variation in species richness than other variables. Moulder and Reichle (1972) have demonstrated that prey capture and energy acquisition by forest litter spiders is greatest in the spring months, a period of rapid growth and maturity for many species. It appears that in the early months of the growing season, the relationship between species richness and litter depth can best be explained by the productivity hypothesis (MacArthur, 1965; Pianka, 1974). Areas with more abundant prey offer more prey choice to foraging predators like wandering spiders, and may allow greater specialization than less productive areas. Because each species may utilize less than the total range of available foods, more species may coexist.

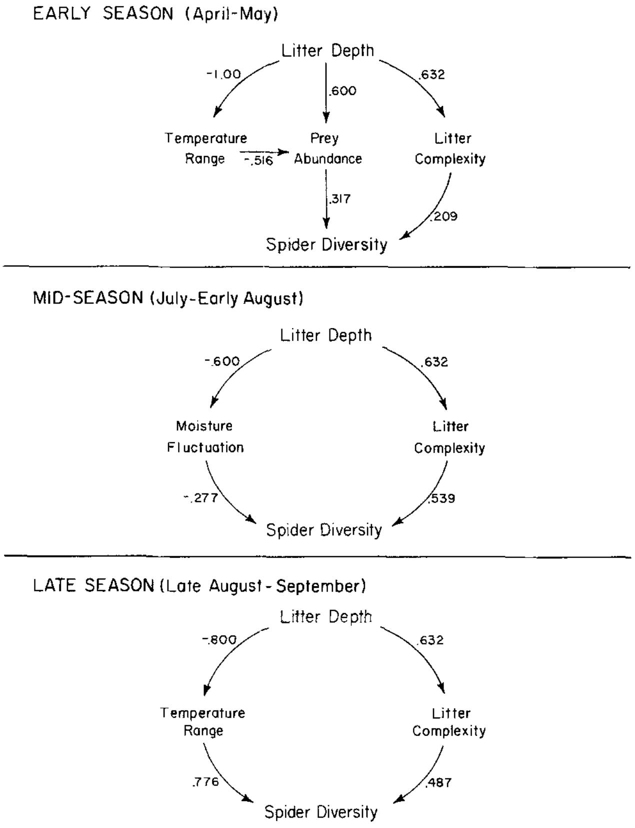

Fig. 5. Partial correlation analysis of variables associated with litter depth and spider species richness, based on blocks of data from three times of the growing season. Upper rows of numbers are initial rank correlation coefficients (Kendall's tau). Lower rows are partial and multiple-partial coefficients

In mid-season, litter complexity appears to be the most influential variable affecting species richness. Temperatures at this time are universally favorable for activity of spiders and their prey, and prey appear to be equally abundant in all plots. Midsummer weather tends to be hot and dry in central Illinois, so it is possible that microhabitats which provide shade and moisture might be limiting. The relationship between spider diversity and litter depth may at this time be explained by the spatial heterogeneity of the litter environment. Areas with deeper, more complex litter may provide more numerous or more diverse microhabitats for spiders, and thus support a greater number of species. The addition of species with specialized microhabitat requirements in deeper litter (i.e., the Gnaphosids and Thomisids that use rolled up leaves for retreats) provides some evidence of this. Midseason is also the time when many of the species reproduce, and there are large numbers of immature spiders foraging in the litter. Spatial heterogeneity in more complex litter may provide refuges from inter- and intra-specific predation, allowing less abundant species to persist in patches. Edgar (1969) found that an experimental three-dimensional litter substrate reduced cannibalism in wolf spiders. Also, it is possible that more species could partition a complex litter habitat vertically. The shift in dominance from Lycosidae to other families over gradients of litter depth and structure suggest that complex litter may prevent competitive exclusion of species that forage within litter rather than on the surface. Increased complexity of litter has been shown to influence the diversity of all litter-dwelling arthropods (Duffey, 1975; Anderson, 1957) resulting in a more diverse array of prey resources for spiders, which in turn may allow more species to coexist. Karr (1975) suggests that complexity of energy packaging influences diversity, and that diversity is greater where food resources (e.g. prey arthropods) occur in a diverse array.

In the late season, it appears that temperature variation is the primary factor influencing species richness. Reduction in the breadth of the seasonal species richness curve and absence of spiders in plots where litter was removed suggests that the physical environment plays a major role in determining species richness. At this time of the year, the relationship between species richness and litter depth can best be explained by a hypothesis that considers environmental stress. Stability of the physical environment has been discussed as a promoter of diversity (Janzen, 1967; Sanders, 1969), but largely in relation to diversity over latitudinal gradients or evolutionary time scales. Since litter depth is likely to change in any particular patch from year to year, explanations invoking the stability-time hypothesis are not entirely appropriate. It is logical that (as suggested by this hypothesis) in habitats with extreme fluctuations in aspects of the physical environment (especially temperature), animals will expend a disproportionate amount of energy on maintenance, and have little left for reproduction and/or adaptive specialization. Most of the species collected in these studies overwinter in penultimate instars, and die in midsummer after leaving eggs (or rearing young past the second instar). Thus, it would be expected that species would "drop out" of the active spider community as soon as their developmental requirements were met. Selection would favor individuals that completed their life cycle before the low temperatures of the fall restricted their nocturnal foraging time. Since no "new" species with late season occurrence were added to communities, we might assume that areas with deeper litter (and reduced temperature variations) permit prolonged seasonal activity of species already present, or reduce mortality due to temperature stress (Williams, 1962). Areas where the insulating effect of litter serves to prolong arthropod activity have, in effect, greater prey abundance (Riechert and Tracy, 1975; Gill, 1969). This would also increase survivorship of late season "stragglers", and increase the number of species collected over the whole season.

Conclusions

The influence of heterogeneous environments on the structure of animal communities has been discussed frequently in the ecological literature. Studies have demonstrated a correlation between structural complexity of habitats and species diversity in birds (MacArthur and MacArthur, 1961), lizards (Pianka, 1967), mammals (Rosenzweig and Winakur, 1966), molluscs (Kohn, 1967), crustaceans (Abele, 1974); insects (Murdoch et al., 1972) and terrestrial cave arthropods

(Poulson and Culver, 1969). The manner in which spatial heterogeneity affects community structure varies with animal groups and may depend on the relationship between the animals and the physical attributes of their environment. For example, foliage height diversity of plant communities may affect birds by providing nesting sites or perches and affect insects and other arthropods by varying feeding niches or microhabitats.

Studies of litter-dwelling spiders over gradients of litter depth and structure in three deciduous forests demonstrate that variation in litter habitats affects spider species richness and species composition. Variables affecting the species richness of litter-dwelling spiders, are related to litter depth and include litter complexity, prey abundance, and temperature variation. The variables represent several major factors that are expected to influence animals in any environment: spatial heterogeneity, productivity (of prey), and climatic stability. Since the relative influence of these factors changes during the growing season, it is doubtful that only one factor determines species richness. The number of species present at any place at any time is likely to be determined by a complex of historical and current environmental variables, as well as unique properties of the group of organisms being considered.

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