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The effects of plant species composition and habitat architecture on the organization of spider communities

Monica Lynn Beals

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Susan E. Riechert, Thomas G. Hallam, Major Professor

We have read this thesis and recommend its acceptance:

Mitch Cruzan, James Drake
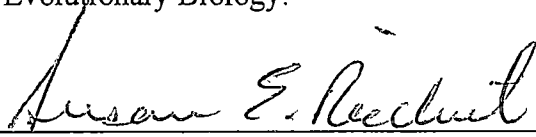
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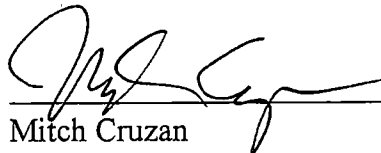
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THE EFFECTS OF PLANT SPECIES COMPOSITION AND HABITAT ARCHITECTURE ON THE ORGANIZATION OF SPIDER COMMUNITIES

A Thesis
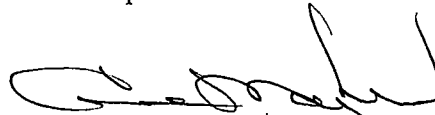Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Monica Lynn Beals
August 2001

ACKNOWLEDGMENTS

I am indebted to my major professor, Dr. Susan Riechert, for her guidance in developing and carrying out this research project, for discussing ideas with me, and for her patience and gentle prodding when necessary. I am grateful to my committee members, Dr. Mitch Cruzan and Dr. James Drake, for their input during the project and their thoughtful review of this thesis.

I am also indebted to my parents and family for their support of my endeavors. They encouraged my intellectual curiosity from a young age, and without their support, understanding and encouragement this project could not have been completed.

I am indebted to many people here at the University of Tennessee. First and foremost, I would like to thank Dr. Patricia Cox for her invaluable assistance in identifying my "ecologist's" plant specimens. Lucinda Hern assisted with data collection during my July 1998 sampling period.

Finally, I would like to extend many thanks to my fellow graduate students in the Ecology and Evolutionary Biology Program, past and present, for providing humor and encouragement when they were most desperately needed. I cannot imagine a more supportive group of colleagues.

ABSTRACT

Substantial empirical evidence in the ecological literature has demonstrated the importance of habitat structure in organizing animal communities. Species abundance and distributions have been shown to respond to a number of habitat structure parameters, including architectural complexity and structural heterogeneity (e.g., patchiness). Previous work in spider communities has indicated that spiders are no exception to this general pattern. Habitat structure is associated with spider species diversity, and different species within a community exhibit varying degrees of preference for specific habitat configurations. At the community level however, few, if any, studies have addressed the relationship between spider communities and plant species composition. This study assesses the relative influences of both habitat structure and plant species composition in three spider communities in East Tennessee.

Data from the current study suggest that the species composition of the vegetation plays a prominent role in spider community organization. Results from Mantel tests indicate a stronger relationship between spider and plant species assemblages than between spider assemblages and habitat configurations. While species diversity and densities in these communities were significantly predicted by habitat structure, six of the twelve abundant species considered individually were significantly associated with plant species composition. Only three species were associated with habitat. The plant species may have reflected variations in habitat structure at a finer scale than that captured by the specific habitat measurements made in this study.

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I. INTRODUCTION

The patterns and processes underlying community structure, or organization, are not well understood. Despite a wealth of studies, the inherent complexities and the multivariate nature of communities have challenged researchers' abilities to tease out their fundamental organizing principles. At its simplest, community structure can be defined as both the number and types of species present, as well as their relative abundances (i.e., number of individuals per species) (Swihart & Slade 1990). To this definition we might add information about spatial and temporal niche partitioning, inter- and intraspecific interactions, and functional roles of community members.

Patterns of habitat use by species within a community provide an excellent starting point for investigations of the factors influencing community structure. Observed distributions have been hypothesized to result from competition or niche partitioning along a resource gradient (Schoener 1974; Robinson 1981; Wywialowski 1987; Swihart & Slade 1990; Denton & Beebee 1994). Evidence for competition in natural communities, however, has been equivocal (Conley 1976; Rotenberry & Wiens 1980; Horton & Wise 1983; Riechert & Cady 1983; reviewed in Strong *et al.* 1984; Hastings 1987; reviewed [for spiders] in Wise 1993). Distributions of species could also result from preferences of some species for specific habitat features and corresponding lack of preferences by other species (Dueser & Porter 1986; Wywialowski 1987; Friend & Cellier 1990; Seamon & Adler 1996). This thesis explores the habitat association alternative utilizing three spider communities in East Tennessee.

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Habitat Associations

Perhaps the most common approach to measuring habitat utilization patterns by species in a community involves testing for their positive or negative associations with various features of their habitat (e.g., vegetation architecture, microclimate, floristic composition, etc.). The presence of a positive association would indicate that a species is specialized in its habitat usage relative to a particular feature, while the presence of a negative association would indicate avoidance of use, perhaps due to competition or physical limitations. Absence of strong habitat associations suggests that the species is a habitat generalist, though it may be specialized with respect to some other niche parameter (e.g., prey type or size). Wywialowski (1987) provides a good example of species niche partitioning on the basis of habitat utilization patterns. She defined rodent species that consistently preferred greater amounts of habitat cover as specialists, and those species that displayed weaker preferences for greater habitat cover as generalists. The red-backed vole (*Clethrionomys gapperi*, the habitat specialist) was more vulnerable to predation in areas of less cover while the deer mouse (*Peromyscus maniculatus*, the habitat generalist) showed no difference in predation vulnerability between the two cover densities (Wywialowski 1987).

Habitat architecture, particularly structural heterogeneity, has been found to play an important role in the distribution and diversity of many animal groups: e.g., birds (MacArthur & MacArthur 1961; Rotenberry & Wiens 1980, among many others), wandering spiders (Uetz 1979), web-building spiders (Greenstone 1984; Rypstra 1986;

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Gunnarsson 1988; but cf. Ralph 1985), freshwater gastropods (Brönmark 1985), lizards (Friend & Cellier 1990), and sap-feeding insects (reviewed in Denno & Roderick 1991). Since habitat selection is thought to affect fitness in part by reducing interspecific competition (Kronk & Riechert 1979), heterogeneous habitats that offer more habitat choices might be expected to support greater species numbers. In addition to a greater number of habitat choices, Uetz (1979) suggests that heterogeneous habitats also provide a greater range of prey types (see also Hatley & MacMahon 1980; Denno & Roderick 1991). Habitat heterogeneity may also enable rare species to persist by reducing chance of encounter and consequent opportunity for interspecific predation (Uetz 1979), or when coupled with differential habitat preferences of species within guilds, may mitigate interguild competition, thus allowing greater numbers of species to coexist in a given habitat (Hatley & MacMahon 1980; Robinson 1981).

Results from some community studies, however, have led to the conclusion that habitat structure is less important in determining species distributions and abundance than is the floristic composition of the habitat. Wiens and Rotenberry (1981), for example, examined data from a study of shrub-steppe bird communities (a regional-scale study, as opposed to the 'continental'-scale study of Rotenberry & Wiens 1980) and found strong correlations between bird species composition and plant species composition. The authors suggested that on a coarse scale birds did indeed respond to habitat structure, but that within habitat types they responded to floristic composition. Further evidence for this view was garnered by analyses of grassland bird assemblages (Rotenberry 1985). Bird species composition was significantly associated with plant species composition but

not habitat structure, even after accounting for the significant association between plant species and structure (a relationship that is hardly unexpected).

Other work has indicated that in some cases animals appear to be distributed independently of both habitat structure and plant species composition. Koen and Crowe (1987) sampled three forest types in the Cape Province of South Africa to determine the effects of floristic and structural differences on both bird and invertebrate communities, and to investigate the possibility of using these communities as indicators in forest management practices. Although the three forest types were quite distinct based on the habitat parameters (i.e., plant species composition and habitat structure), there was no distinction based on the bird communities. The ground surface invertebrates exhibited distinct patterns of association with habitat structure and floristic composition in the same study, but the litter and aerial invertebrates did not, and the authors concluded that overall the invertebrate communities were of limited utility in differentiating among the forest types. Their results indicate that in this region, floristic composition and habitat structure play minor roles in determining bird and invertebrate community structure.

Spider Community Structure

Empirical studies of habitat associations that have attempted to distinguish among the many factors potentially influencing spider community structure (plant structural variability, prey abundance, etc.) have generally concluded that vegetation architecture is the best predictor for species diversity. For example, Hatley and MacMahon (1980) found that the architectural complexity of experimentally manipulated vegetation was a significant determinant of spider community structure: species and guild diversities were

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significantly higher in the more structurally complex shrubs. In another study, the diversity of web-building spiders was significantly predicted by a simple measure of habitat heterogeneity (vegetation tip height diversity), but not by prey availability (Greenstone 1984). Similarly, Lisken (1988) was able to discriminate between the effects of vegetation structure versus prey abundance and diversity in prairie spider communities, and found that vegetation structure was the best predictor of spider diversity. Vegetation architecture appears to be a good predictor for spider densities as well. Balfour and Rypstra (1998) found that higher weed densities were correlated with higher web spider densities, indicating that more web attachment sites were available as the vegetation became more structurally complex.

Studies that have investigated the distribution patterns of individual spider species and guilds in relation to habitat architecture have concluded that spiders belonging to the same guild (i.e., groups of species or families that employ similar foraging strategies; see Root 1967) respond to different environmental factors. For instance, Turner & Polis (1979) found that members within the ambush-hunting guild exhibited preferences for different microhabitat features. Hatley & MacMahon (1980) demonstrated by manipulating shrub foliage density that denser shrubs supported significantly higher numbers of spider species, with greater abundances of jumping spiders (ambush hunting guild) in clipped and control shrubs, and greater abundances of web-builders in denser shrubs. Robinson (1981) found that while many spider species exhibited preferences based on fine-grained architectural features of artificial habitat modules, members of some guilds did not appear to discriminate between different configurations of substrates in the artificial structures. In another study litter structural complexity had considerably

less influence on overall community organization than did litter depth; however, litter structural complexity significantly affected web-building spider abundance, perhaps because of the need for web attachment sites (Bultman & Uetz 1982). Spider species within guilds and guilds themselves clearly respond differently to the various components of habitat architecture.

Project Goals and Rationale

The goal of the current study is to use Post and Riechert's (1977) sampling protocol to describe community structure for the three spider communities in which they investigated spider species interactions with one another, but did not specifically address patterns of species interactions with their environment. These data will be used to determine the roles of habitat architecture and plant species composition in shaping these three spider communities. I have addressed the following questions:

Q1:   Are the three sites distinguishable on the basis of unique habitat configurations or plant species assemblages?

Q2:   How and to what extent are the spider communities of these three sites influenced by unique habitat configurations or plant species assemblages?

Q3:   How do individual spider species respond to habitat and plant species assemblages?

Spider communities are made up of a number of guilds that can be defined at the most general level as trap (i.e., web-building) predators, ambush hunters, and active

hunters. The broad definitions of these guilds make spider communities potential model systems from which conclusions about influences on community structure might reasonably be generalized to other predatory taxa (Wise 1984, 1993; Terborgh & Robinson 1986; Uetz 1991). Insights from the current study will hopefully contribute in small part to our understanding of this complex subject, and perhaps add perspective to the information provided by commonly applied measures of habitat utilization.

II. METHODS

Study Area

This study was conducted in Knox County, Tennessee in a woodlot owned by the University of Tennessee (35° N 83° W). The climate is temperate, with mean daily temperatures ranging from 17° C to 28° C in the summer months (May through September), and annual precipitation averaging 119.74 cm, approximately 40% of which falls during the summer (National Climatic Data Center).

The three adjacent sites in the University of Tennessee woodlot used in this study had been previously sampled for spiders in July 1975 to examine spider species interactions (Post & Riechert 1977). Each site represents a different habitat type: a sloped field, a tussock grass field, and a deciduous woodland. Scientific names of plants are taken from Wofford (1989).

Site Descriptions

The old field habitat designated as Site 1 ("sloped field") is maintained by periodic mowing. The slope of the northeast-facing hill is steepest near the top (15%) and gentlest (5%) at its base. The sloped field is dominated by the grasses *Dactylis glomerata* L. and *Microstegium vimineum* (Trin.) Camus, and the perennial herb *Desmodium* sp. Several other perennial herbs (*Convulvulus arvensis* L., *Verbesina* sp., *Vernonia gigantea* (Walt.) Trelease ex Branner & Coville, and *Lysimachia nummularia* L.) are abundant at the site as well.

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The tussock grass field designated as Site 2 is in a level area subject to flooding located at the southeastern end of the sloped field and separated from it by a band of shrubs (approximately 7m wide). It is bordered to its southeast by a marshy area, and to its southwest by a creek. This area is not mowed and is generally flooded at least once each spring and drains slowly, usually drying out by mid-June. The annual herb *Polygonum* sp., the perennial herbs *Glecoma hederacea* L. and *Lysimachia nummularia* L., and the grass *Festuca* sp. dominate the vegetation in the tussock grass field. Other abundant species are the perennial herbs *Solidago canadensis* L., *Boehmeria cylindrica* (L.) Sw., and *Convulvulus arvensis* L., the sedge *Carex* sp., and the annual herb *Impatiens capensis* Meerb. Plant species in the tussock grass field tend to be more clumped in Site 2 than in Site 1. Some areas of the tussock field are composed almost exclusively of one or two species.

Site 3 is a deciduous woodland located immediately to the southwest of the sloped field. This site consists of two facing slopes separated by a narrow strip of wet mesic bottomland (varying from approximately three to ten meters in width). The canopy is dominated by *Liriodendron tulipifera* L. (tulip poplar) and *Quercus rubra* L. (northern red oak), with occasional beech (*Fagus grandifolia* Ehrh.), chestnut oak (*Q. montana* L.), black walnut (*Juglans nigra* L.), bitternut hickory (*Carya cordiformis* [Wang.] K. Koch) and black gum (*Nyssa sylvatica* Marsh.). The understory is dominated by maple (*Acer* sp.) and box elder (*Acer negundo* L.) with a few *Ulmus rubra* Muhl. (slippery elm). The shrub layer is sparse and consists of only a few shrubs dispersed throughout the site (*Lindera benzoin* [L.] Blume and *Lonicera* sp.). The herbaceous layer on the slopes is dominated by *Toxicodendron radicans* (L.) Kuntze, *Bignonia capreolata* L., and

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Euonymus sp., while that of the bottomland is composed primarily of *Microstegium vimineum* (Trin.) Camus and *Pilea pumila* (L.) Gray.

Sampling methods

I sampled each of the three sites, representing different habitats, at two different times of year in consecutive years: from 3 July to 18 July 1997, from 23 August to 8 September 1997, from 10 July to 29 July 1998, and from 24 August to 20 September 1998. This resulted in a total of 12 habitat × season × year (HSY) samples.

Within each site, circular quadrats ($0.1 \ m^2$) were located using the random walk method based on Catana 1955. In the center of each site I tossed a coin twice to select my initial direction (i.e., the first toss determined North/South or East/West and the second toss determined either North or East, or South or West). The number of steps walked in the chosen direction was determined by a random number table. After locating a quadrat this procedure was repeated using that quadrat as the starting point. After the initial selection of direction, I alternated between a North/South and East/West trajectory; in other words, if the initial direction for locating the first quadrat was North, the second quadrat would be either East or West of the first depending on the coin toss, the third quadrat would be either North or South of the second, and so on. If the edge of a site was reached I reversed course and continued walking until I had completed the appropriate number of steps.

A flag was placed in the center of each quadrat to mark its location. In both sampling periods in the preliminary year of sampling (1997) 20 quadrats were located in

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each site (total = 120 quadrats). To ensure adequate sample sizes the following year, the number of quadrats sampled was determined by calculating the standard error of the mean number of individuals collected in the first five quadrats, adding quadrats five at a time, and recalculating the standard error at each step. When the standard error of the mean number of individuals no longer decreased with the addition of more samples, the sample size was considered adequate (Post & Riechert 1977). Based on this, 35 quadrats were sampled in the sloped field during each period in 1998, 30 quadrats were sampled in the tussock grass field, and 20 quadrats were sampled in the deciduous woodland (there was no seasonal variation apparent in the number of quadrats required for adequate sampling).

Vegetation Sampling

Measurements of habitat variables were taken at least one day in advance of spider sampling to minimize disturbance to the spiders. In each site data were recorded for the following variables:

Density An index of density was used. A thin dowel rod marked in one-centimeter increments was placed upright in the center of each quadrat, and the lowest height at which at least one full centimeter was visible through the vegetation was recorded.

Intervals This variable is a measure of habitat architecture, modeled after the point-intercept method of estimating plant species cover (Heady *et al.* 1959). Two dowel rods (0.9 cm diameter) were placed upright at either end of a north/south or east/west axis through each quadrat (the direction of the axis was determined randomly). The poles had metal loops projecting outward every 10 centimeters. At each 10-centimeter increment

above the ground, small rods (0.3 cm diameter) divided into seven five-centimeter intervals were placed through the loops on the two poles (Figure 1), and the number of intervals in contact with vegetation at each height was recorded. Ordination scores based on these values were used to represent the relative quantities of open space in a quadrat.

Vegetation Height Each quadrat was divided into four quarters: NW, NE, SW, and SE. In each quarter, the height of the tallest plant was measured, and the mean, standard deviation, and coefficient of variation were calculated.

Vegetation Cover A lightweight wire ring 0.1 m^2 was used to outline each quadrat, and a small cardboard square (49 cm^2, approximately 5% of a 0.1 m^2 circle) was used to estimate percent cover for each plant species. These data were used to calculate diversity and evenness indices, to perform ordination analyses, and to quantify the total surface area of plants grouped based on physiognomic characteristics within a quadrat (i.e., the total surface area of plants with hirsute leaves, or the total surface area of grasses, herbs, etc.).

Spider Sampling

Spider collections were completed on clear days between 10am and 3pm. Sampling was limited to days on which no measurable precipitation occurred during the six hours prior to beginning sampling. Each quadrat was approached slowly, and care was taken to minimize the disruption of vegetation that might cause spiders to be disturbed in or near the quadrat. When within two to three feet of the quadrat, I waited remaining as still as possible for a few minutes to allow any displaced spiders to return to the area.
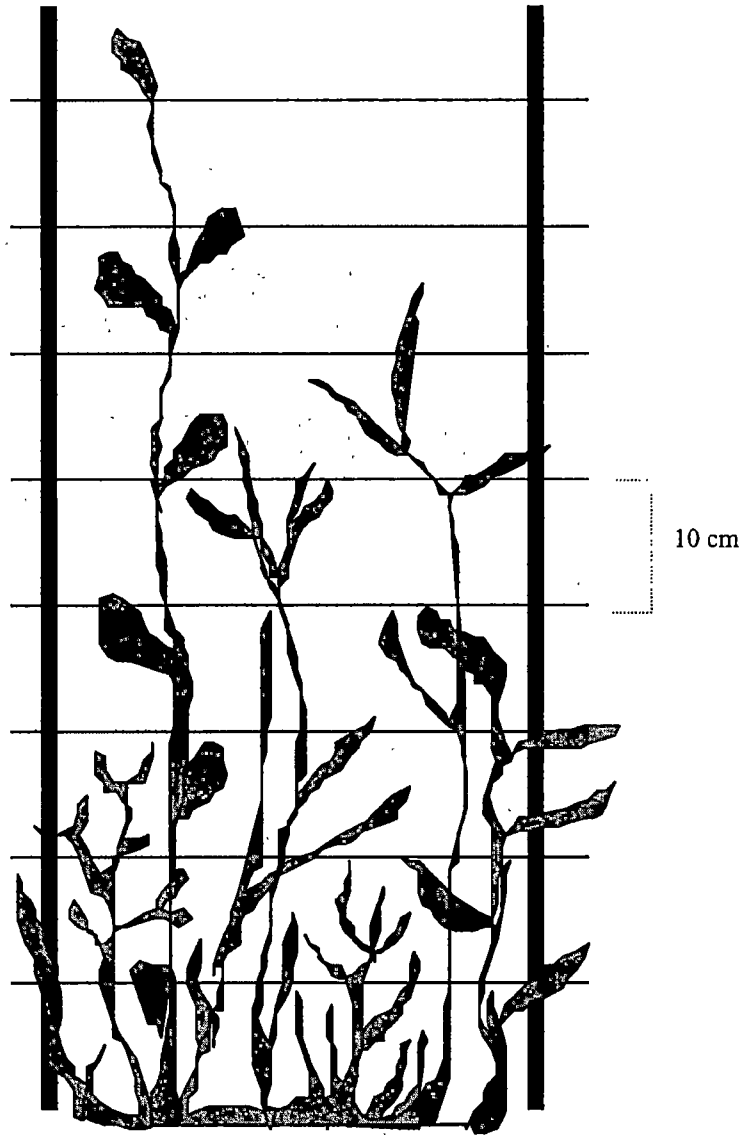
Figure 1. Device used to record interval data. Each horizontal dowel rod was divided into seven 5 cm intervals and placed through metal loops at 10 cm height increments. The number of 5 cm intervals in contact with vegetation at each height was recorded.

I used a metal cylinder (0.38 m high, 0.1 m^2 [~ 0.35 m diameter]) to collect spiders. The interior of the cylinder had been painted white to facilitate locating individuals crawling up the side. At each quadrat location the cylinder was firmly pushed into the soil after sticks that kept the bottom of the cylinder off the ground were quickly removed. Any vegetation within the quadrat that was taller than the height of the cylinder was immediately broken or bent, and the marker flag was removed.

The vegetation and walls of the cylinder were visually inspected for spiders; those found were removed with a handheld aspirator and placed in a vial containing 70% ethyl alcohol. The vegetation (and/or litter) was then carefully removed from the quadrat and placed in a plastic bag. Additional spiders found during this process were deposited in the vial. When all of the vegetation had been removed the bag was sealed and labeled, and the bare ground and walls of the cylinder were scanned once more for spiders. Plastic bags containing the litter and vials of ethanol were stored in the shade while the remaining samples were collected.

The vegetation collected from each site was transported to the lab where the contents were sorted on a white sheet within 24 hours of collection. I refrigerated these samples for a minimum of 10 minutes prior to sorting to retard spider activity. Spiders found during sorting were added to the sample collected from the corresponding quadrat in the field.

Spiders were subsequently identified to species where possible. Early instars that could not be identified to species were identified to genus. When a genus was represented by a single species in all three study areas during all four sampling periods, juveniles of that genus were assumed to belong to that same species.

Descriptive Statistics

Diversity

Spider communities in the three habitats were compared using several indices. Roth *et al.* (1994) suggested that since each diversity index has its own suite of strengths and weaknesses, the ideal approach would be to apply several indices to the same dataset. To compare the diversity of both spiders and plants among the three communities, seasonally, and from year to year, I chose the Shannon-Wiener index (Shannon & Weaver 1949) and its components of diversity, species richness (the absolute number of species present in a given area) and equitability (the evenness with which individuals are distributed among species). Note that I initially also employed the unbiased form of Simpson's index (Rosenzweig 1995; Simpson 1949) which is independent of sample size and does not assume a particular abundance distribution. However, I present only Shannon-Wiener here as the results of both indices were highly correlated ($r = 0.90$) and the Shannon-Wiener index is more widely used.

The Shannon-Wiener diversity index (H'), which is derived from information theory, is:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where p_i is the proportion of the community making up the ith species. Higher values for H' indicate greater diversity. The Shannon-Wiener estimate of equitability is:

$$E_{H'} = H'/H'_{max} = H'/\ln S$$

where H'_{max} is the value H' would assume if individuals were distributed in exactly equal proportions among the species (in which case equitability would be 1). This maximum value is equivalent to the natural log of the total number of species, S. The Shannon-Wiener index, species richness, and equitability were also calculated for both plants and spiders within individual quadrats and used in regression analyses (see "Habitat Associations" below).

Habitat Associations

I employed several analyses to examine spider species' associations with vegetation and habitat features. As is common in community ecology, the data matrix for both the spiders and vegetation was sparse, containing many zeroes. A large number of plant and spider species were observed, but in each sample unit only a small proportion of those species was present. This made otherwise appropriate analyses (e.g., regression techniques) of the raw data statistically intractable. Unfortunately, the fact of a sparse data matrix also precluded the application of many multivariate techniques for variable reduction, such as cluster or factor analyses.

This problem was addressed in part by subsuming species into physiognomic categories in the case of the plants. The percent cover data for plant species were used to create classes within two new metrics: hirsuteness and growth form. Each plant species was characterized on a scale of hirsuteness (3 = leaves and stems hirsute, 2 = leaves only hirsute, 1 = stems only hirsute, and 0 = leaves and stems glabrous) and growth form (3 = shrub/tree, 2 = herb/fern, 1 = grass/sedge, and 0 = vine/creeping or trailing herb) based on

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literature descriptions (Gleason & Cronquist 1991, Holmgren 1998, Newcomb 1977, Wofford 1989), and the species were grouped by these classes for each metric. The total surface area of plants within a quadrat for a given class was calculated by multiplying the sum of the percent cover of species in that class by 0.001 m^2 (given that 1% of a 0.1 m^2 area is approximately equal to 0.001 m^2). These values were included with the other habitat variables in ordination analyses.

Ordination Analyses

To investigate whether the three sites were distinguishable on the basis of unique habitat configurations, plant species assemblages, or spider species assemblages (Q1) I employed Bray-Curtis ordination, as computed by PC-ORD (McCune & Mefford 1999), to visualize the interrelationships of spider species, plant species, and habitat. This ordination method was chosen because it has been shown to be superior to other methods (e.g., Principal Components Analysis) in providing a more realistic picture of ecological data (Beals 1984, Gauch & Whittaker 1972, Gauch *et al.* 1977, McCune & Beals 1993). Ordinations were performed separately on the spider, vegetation, and environmental (non-floristic) data, and on the transposed matrix of spider data to look at species in sample space.

Presence/absence data were used for ordinations of the spider and plant species since the use of binary data allows one to transform the data with the "sociological favorability index" or Beals smoothing function (Beals 1984, McCune 1994). This transformation alleviates the "zero truncation problem" (Beals 1984) in which the absence of a species from a sample unit provides minimal information about the

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favorability of the sample unit for that species. In other words, a value of zero for a given species may either be a sampling zero in which case the species is absent by chance, or a structural zero in which case the species could not possibly be present. The Beals smoothing function replaces the original binary value for a species in each sample unit with the probability of that species occurring in the sample unit based on its co-occurrence in other sample units with species that do occur in the sample unit under consideration.

The environmental, or habitat, ordinations included the following variables: vegetation density; mean and standard deviation of the four tallest plants; ordination scores from the interval data; plant species richness; plant species diversity (H') and equitability ($E_{H'}$); total surface area of vines, grasses, herbs, and shrubs; and total surface area of plants within each of the four hirsuteness classes.

Mantel Test

To address the question of how and to what extent spider communities are influenced by habitat structure and plant assemblages (Q2), I applied the Mantel test in PC-ORD (McCune & Mefford 1999) to determine whether the degree of association between pairs of distance, or dissimilarity, matrices were greater than expected by chance. This is a non-parametric, multivariate test that avoids the problems caused by lack of independence among cells in the distance matrices (Mantel 1967; Douglas & Endler 1982; Rotenberry 1985). The dissimilarity matrices were derived from the matrices of plant species, spider species, and habitat variables used in ordination analyses. The dissimilarity measure used was the Relative Sørensen distance, or

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"relativized Manhattan," a measure that has been found to provide ecologically meaningful distance relationships (Faith *et al.* 1987). Significant congruence of any two matrices could suggest a strong relationship between, for example, spider species composition and habitat structure. Matrices must be of equal dimensions for the Mantel test; as a result of missing values for some quadrats in each initial data matrix, a the total number of quadrats used in the Mantel test calculations was 261.

Regression Analyses

Using the scores obtained from the ordination analyses I employed two regression techniques (multiple linear regression and logistic regression) to determine how both spider communities (Q2) and individual spider species (Q3) respond to vegetation composition and habitat structure. I ran multiple linear regressions using PROC REG in SAS Version 8.1 (SAS Institute Inc.) using the following five dependent variables: the number of individual spiders per quadrat, the number of species per quadrat (= species richness), the diversity and evenness of species in each quadrat (using Shannon-Wiener's index), and the number of guilds present in each quadrat (= guild richness). The independent variables were the scores from the ordination axes calculated for plant species and habitat features.

To investigate the roles, if any, played by plant species assemblages or habitat configurations in determining the presence or absence of individual species, I used logistic regression (PROC LOGISTIC in SAS, Version 8.1, The SAS Institute, Inc.) rather than multiple linear regression. For most species multiple individuals were rarely found together in a quadrat, so species were recorded as present or absent. Such binary

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response variables are appropriate for logistic regression. Species abundance data were transformed to presence/absence data, and logistic regression was performed with the independent variables listed above. I set the cutoff for determining which species were included in regression analyses as those that were represented in a minimum of 10% of the quadrats.

III. RESULTS

Descriptive Statistics

The sloped and tussock grass fields had higher mean numbers of spider individuals per quadrat than did the deciduous woodland (Table 1), though there was considerable variability from one sampling period to the next, particularly in the former two sites. Spider and plant species lists are presented in the Appendix, Tables 7 and 8, respectively.

Diversity

The Shannon-Wiener index of species diversity produced a different view of spider diversity among habitats than did the simple measure of species richness (Table 2). The sloped field has the highest mean species richness (S) ($\bar{x}_S = 40.50$), followed by the tussock grass field ($\bar{x}_S = 32.00$) and the deciduous woodland ($\bar{x}_S = 28.75$). The Shannon-Wiener index, which accounts for both the abundance and evenness of individuals among species, on the other hand, showed the opposite pattern. The deciduous woodland is the most diverse habitat based on Shannon-Wiener's index (H'), with $\bar{x}_{H'} = 1.24$. This site also has the highest equitability values ($\bar{x}_{E_{H'}} = 0.85$), indicating that the evenness of distribution of individuals among species in the deciduous woodland is the factor primarily accounting for these high values of the diversity index. The means for plant species richness in the sloped field and tussock grass field were

Table 1

Basic Sampling Statistics. N refers to number of $0.1m^2$ quadrats sampled.
CV = coefficient of variation $((S.E. / \bar{x}) \times 100)$ (Sokal & Rohlf 1995)

	Sloped Field	Tussock Grass Field	Deciduous Woodland
July 1997			
N	20	20	20
Mean # individuals ($\bar{x}$)	6.30	6.65	4.05
Standard Error (S.E.)	0.91	0.74	0.62
CV	14.44	11.13	15.31
September 1997			
N	20	20	20
Mean # individuals ($\bar{x}$)	7.95	20.05	5.80
Standard Error (S.E.)	1.06	2.19	0.90
CV	13.33	10.92	15.60
July 1998			
N	35	30	20
Mean # individuals ($\bar{x}$)	9.31	3.70	4.55
Standard Error (S.E.)	0.80	0.54	0.68
CV	8.62	14.67	14.91
September 1998			
N	33	30	20
Mean # individuals ($\bar{x}$)	15.39	6.00	5.25
Standard Error (S.E.)	1.78	0.70	0.50
CV	11.57	11.75	9.46

Table 2

Species Diversity Estimates for Three Spider Communities.
Estimates are Presented by Month and Year for Each Site.

	S	H'	$E_{H'}$
Sloped Field			
July 1997	30.00	1.24	0.84
September 1997	48.00	0.99	0.59
July 1998	40.00	1.25	0.78
September 1998	44.00	1.07	0.65
mean	40.50	1.14	0.71
Tussock Grass Field			
July 1997	33.00	1.28	0.84
September 1997	39.00	1.16	0.73
July 1998	24.00	1.06	0.77
September 1998	32.00	1.21	0.80
mean	32.00	1.18	0.79
Deciduous Woodland			
July 1997	24.00	1.20	0.87
September 1997	29.00	1.24	0.85
July 1998	31.00	1.29	0.86
September 1998	31.00	1.23	0.83
mean	28.75	1.24	0.85

S = species richness
H' = Shannon Wiener diversity index
$E_{H'}$ = Shannon Wiener equitability index

similar ($\bar{x}_S$ = 4.44 and 4.89, respectively) and both higher than that of the deciduous

woodland ($\bar{x}_S$ = 2.45). However, because percent cover does not necessarily reflect the

number of plant individuals present, H' could not be calculated.

Habitat associations

Ordination Analyses

Bray-Curtis ordinations were performed on the plant species, spider species, and

habitat variables to provide a visual arrangement of quadrats in plant, spider, and habitat

space, and to determine if patterns were concordant (i.e., if there are patterns within or

between habitats, are these patterns similar for the three datasets?). Beals smoothing

requires the omission of rows (i.e., quadrats) in which there are no observations; quadrats

in which no spiders were present were omitted, as were those quadrats (exclusively in the

deciduous woodland) in which no plants were present. For the ordination of plant species

n = 280, for the ordination of spider species n = 281, and for the habitat ordinations n =

280[a].

The two ordination axes for the plant species (B-C$_P$ 1 and B-C$_P$ 2) demonstrate

clear distinctions among the three sites (Figure 2). These two axes explained 41.74% and

26.98% of the variance among the quadrats respectively (cumulative percent of variance

explained = 68.72%). A third axis (B-C$_P$ 3) was initially computed, but as it explained

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[a] Beals smoothing was not performed on the habitat data since they were not binary. Quadrats in which no plants were present had missing values for species diversity and evenness in the habitat dataset and were therefore omitted as well.
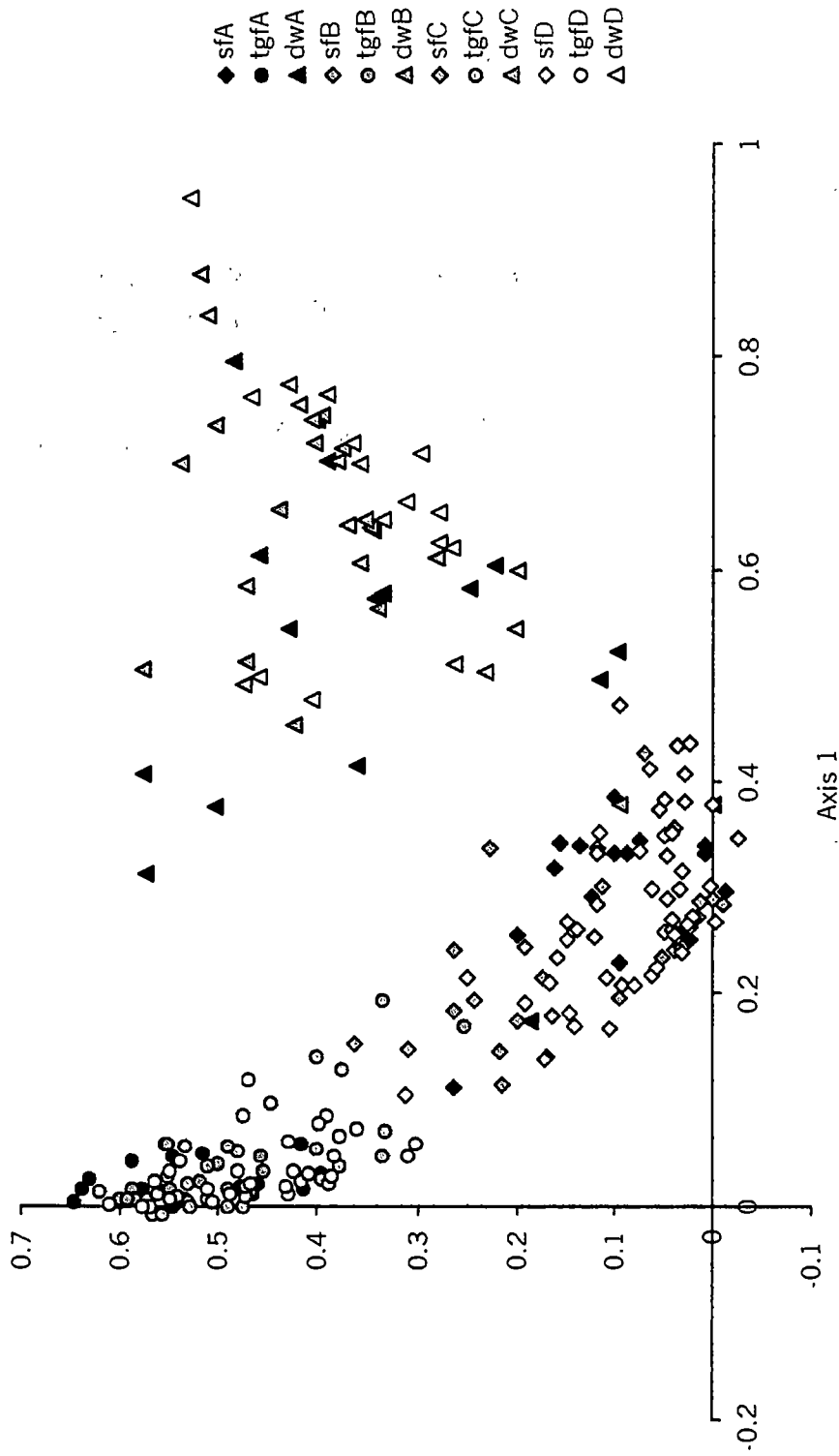
Figure 2. Graph of first two axes of Bray-Curtis ordination scores for quadrats based on plant species presence/absence data (smoothed). "sf" = Sloped Field, "tgf" = Tussock Grass Field, "dw" = Deciduous Woodland, "A" and "B" = 1997, "C" and "D" = 1998, "A" and "C" = July, and "B" and "D" = September.

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less than 10% (4.66%) of the variance it was not included in the final ordination. The three sites show marked separation based on plant species composition, although some overlap is apparent, particularly between the sloped and the tussock grass fields. There does not appear to be any within-site separation of the different sampling periods.

The first two axes of the Bray-Curtis ordination of the quadrats based on the spider species (B-C_S 1 and B-C_S 2) do not exhibit such clear distinctions (Figure 3). B-C_S 1 explained 46.05% of the variance, and although B-C_S 2 explained less than 10% (5.77%) of the variance it was included for graphing purposes. The primary separation of quadrats based on the spider species is between the deciduous woodland and the other two sites. Species compositions do not appear to be clearly differentiated between the sloped field and tussock grass field based on this ordination. Again, the different sampling periods within each habitat show no separation.

Habitat variables (physiognomic and architectural) were used in the third ordination. The first two ordination axes (B-C_H 1 and B-C_H 2) explained 58.26% and 26.61% of the variance, respectively (Figure 4). There is virtually no separation among the sites, although many of the deciduous woodland quadrats are grouped toward the right-hand side of the graph. However, a substantial number of the woodland quadrats are found interspersed with quadrats from the two field sites. As in the previous

The third axis (B-C_H 3) explained 12.49% of the variance (graphed with B-C_H 1 in Figure 5); the cumulative percent of variance explained is 97.37%. Although the sites are less clearly separated here, the deciduous woodland is the most distinct. The quadrats exhibit little separation among sites, but as in Figure 4 many of the deciduous woodland quadrats are grouped on the first axis (although again there is considerable overlap with
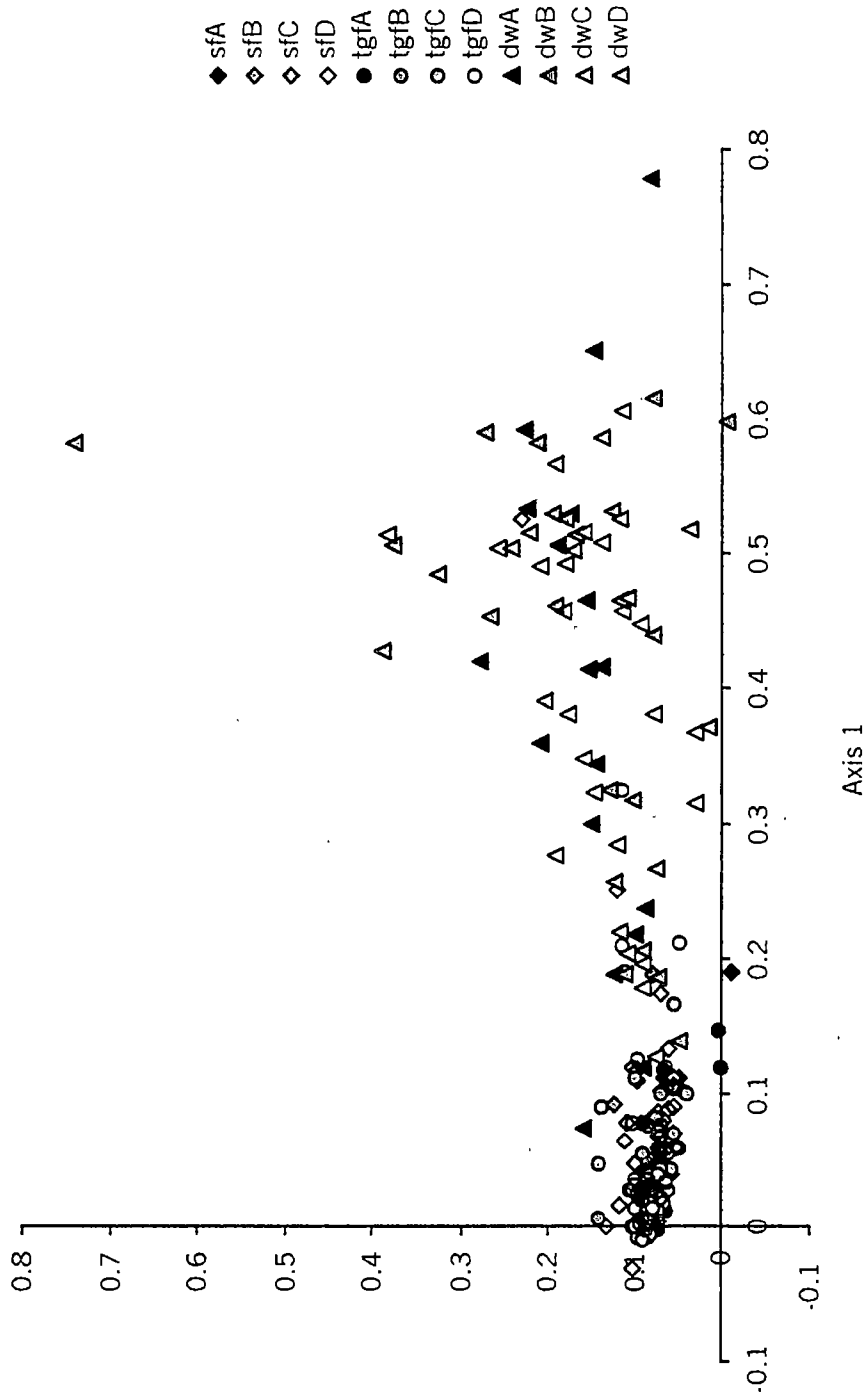
Figure 3. Graph of first two axes of Bray-Curtis ordination scores for quadrats based on spider species presence/absence data (smoothed). "sf" = Sloped Field, "tgf" = Tussock Grass Field, "dw" = Deciduous Woodland, "A" and "B" = 1997, "C" and "D" = 1998, "A" and "C" = July, and "B" and "D" = September.
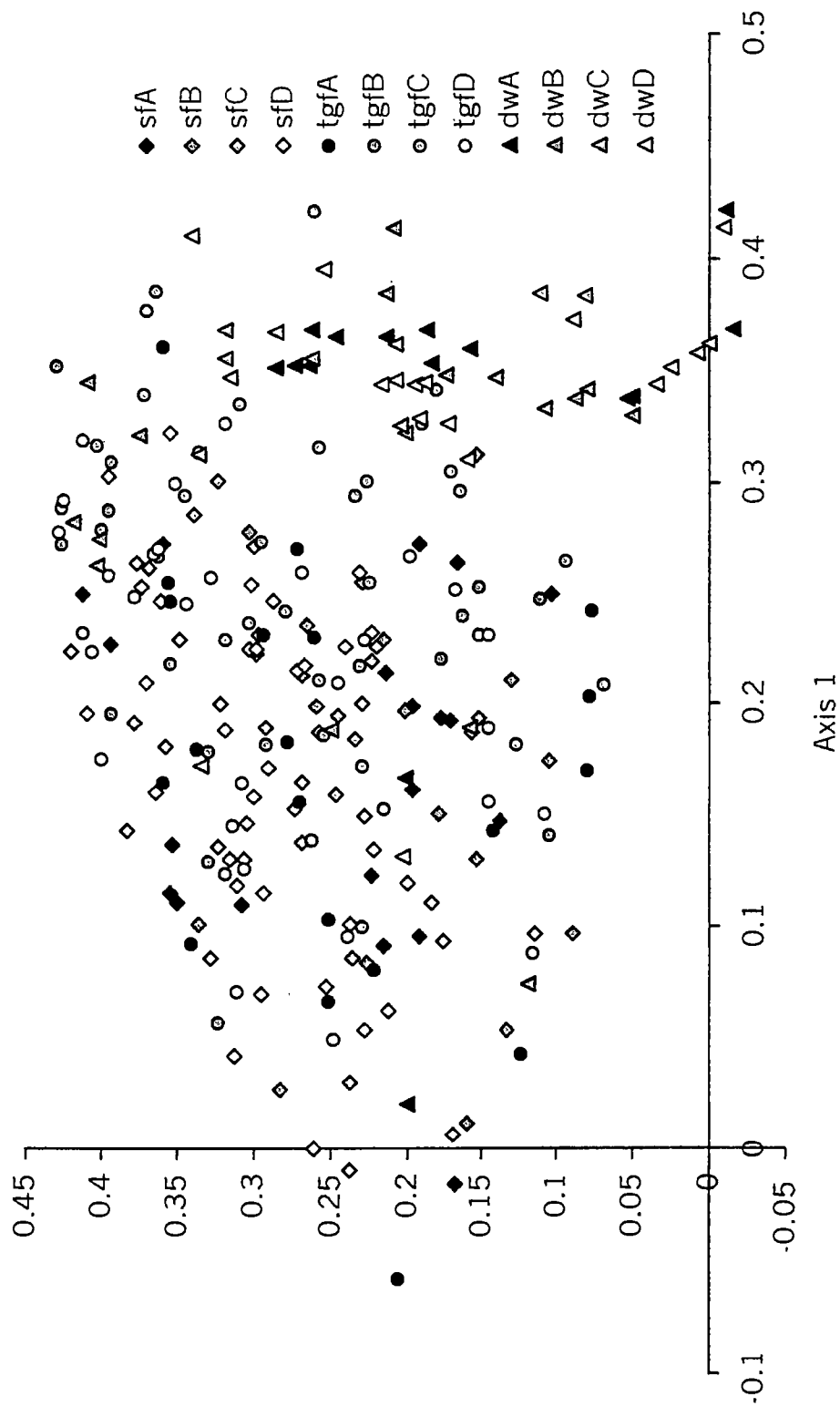
Figure 4. Graph of first two axes of Bray-Curtis ordination scores for quadrats based on habitat variables. "sf" = Sloped Field, "tgf" = Tussock Grass Field, "dw" = Deciduous Woodland, "A" and "B" = 1997, "C" and "D" = 1998, "A" and "C" = July, and "B" and "D" = September.
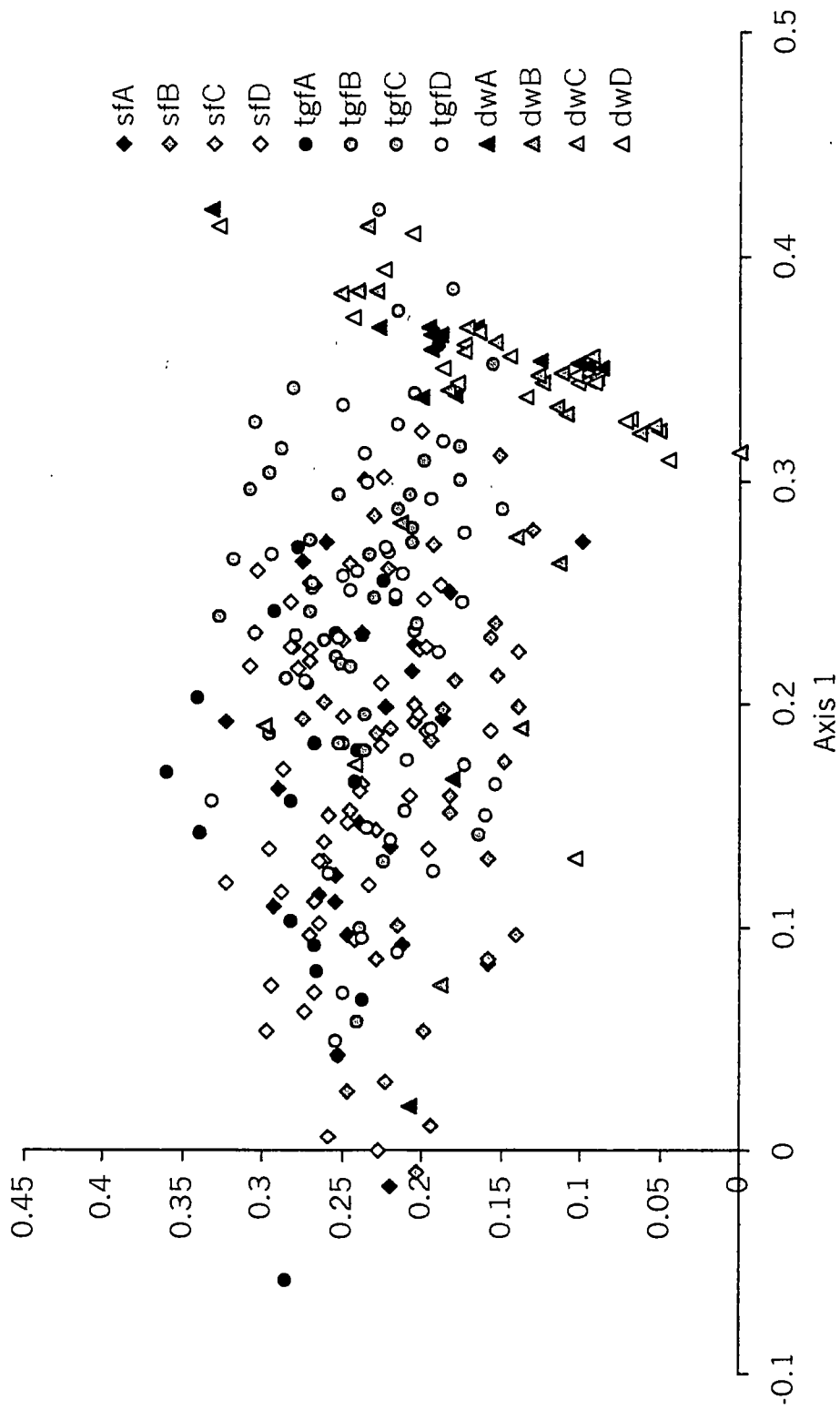
Figure 5. Graph of first and third axes of Bray-Curtis ordination scores for quadrats based on habitat variables. "sf" = Sloped Field, "tgf" = Tussock Grass Field, "dw" = Deciduous Woodland, "A" and "B" = 1997, "C" and "D" = 1998, "A" and "C" = July, and "B" and "D" = September.

the other two sites). B-C$_H$ 3 appears to reflect some separation of the deciduous woodland quadrats as well, but the overall separation of sites based on B-C$_H$ 2 and B-C$_H$ 3 is indistinct (Figure 6).

For the correlations (Kendall's tau-b) between habitat variables and habitat ordination axes an arbitrary cutoff of $|\tau|$ 0.30 was chosen to consider a variable even moderately correlated with an axis (Table 3). Four variables are negatively correlated with B-C$_H$ 1: vegetation density ($\tau = -0.58$), interval ordination axis 1 (a measure of open space within the vegetation) ($\tau = -0.30$), total surface area of grasses/sedges ($\tau = -0.38$), and total surface area of plants with hirsute leaves and stems ($\tau = -0.33$). B-C$_H$ 2 is positively correlated with mean vegetation height ($\tau = 0.45$), and interval ordination axis 1 ($\tau = 0.32$). B-C$_H$ 3 is positively correlated with vegetation density ($\tau = 0.47$), mean vegetation height ($\tau = 0.29$), standard deviation of vegetation height ($\tau = 0.43$), and interval ordination axis 1 ($\tau = 0.34$).

Finally, Bray-Curtis ordination was performed on a transposed matrix of smoothed spider species data to visualize species in quadrat space (as opposed to the usual approach in which quadrats are ordinated in species space). To simplify the ordination only spider species present in 5% or more of the quadrats were included. The first axis (B-C$_T$ 1) explained 54.74% of the variance, and the second axis (B-C$_T$ 2) explained 9.84% of the variance (Figure 7). As with the ordination of quadrats in spider species space (Figure 3), the seven deciduous woodland species (those most abundant in the deciduous woodland, relative to other habitats), represented by triangles, show the
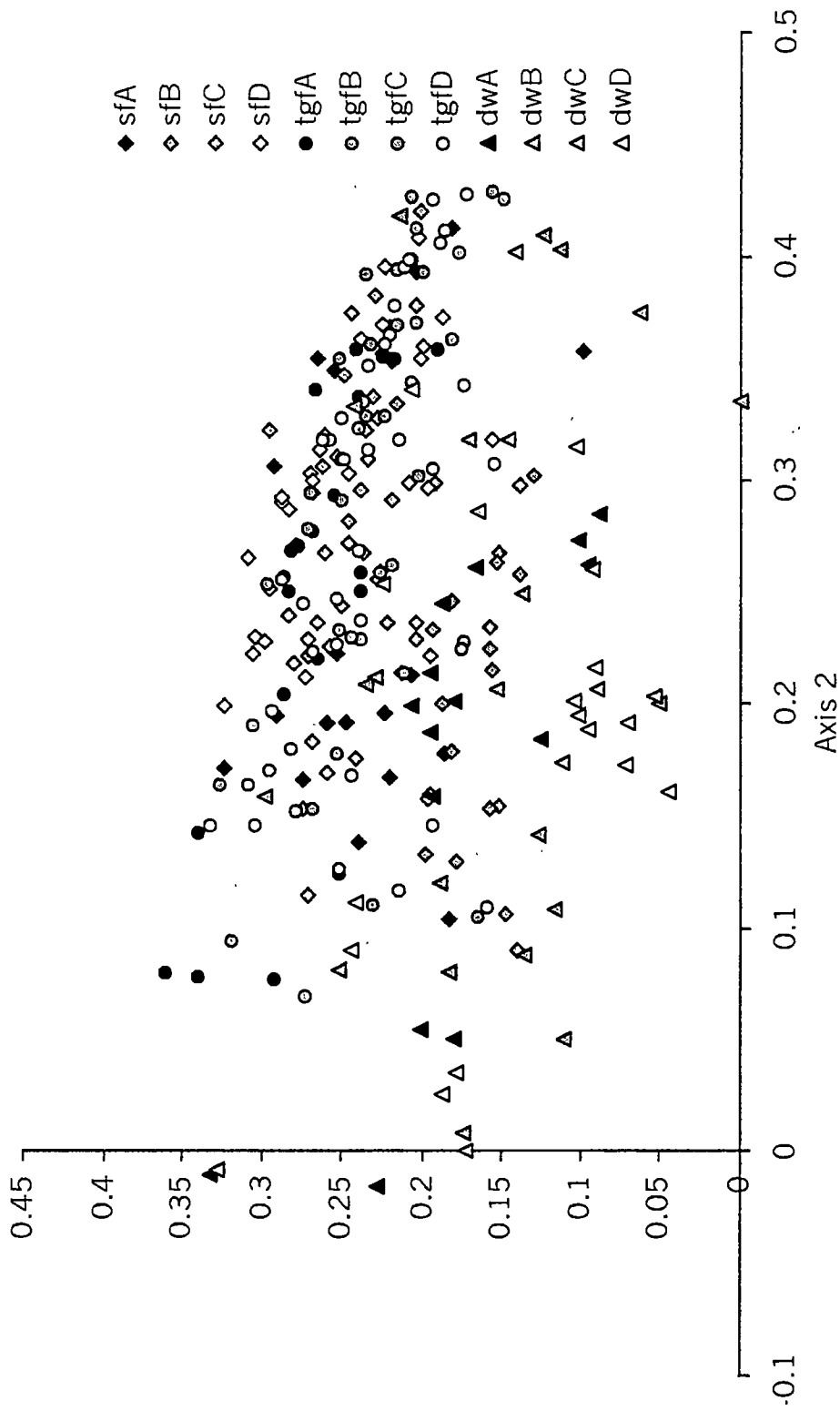
Figure 6. Graph of second and third axes of Bray-Curtis ordination scores for quadrats based on habitat variables. "sf" = Sloped Field, "tgf" = Tussock Grass Field, "dw" = Deciduous Woodland, "A" and "B" = 1997, "C" and "D" = 1998, "A" and "C" = July, and "B" and "D" = September.

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Table 3

Kendall Correlations (tau-b) of Habitat Variables with Bray-Curtis Habitat Ordination Axes

	Axis 1	Axis 2	Axis 3
veg. density	-0.58	0.16	0.47
mean veg. height	-0.03	0.45	0.29
s.d. of veg. ht.	0.20	-0.19	0.43
interval axis 1	-0.30	0.32	0.34
interval axis 2	0.23	0.09	0.01
S (richness)	-0.24	-0.05	-0.03
H' (diversity)	-0.15	-0.02	-0.06
$E_{H'}$ (evenness)	0.03	0.04	-0.10
vines/creeping herbs	-0.02	-0.14	-0.02
grasses/sedges	-0.38	0.09	0.18
herbs/ferns	-0.16	0.25	0.15
shrubs/trees	0.19	-0.10	-0.22
lvs & stms hirsute	-0.33	0.12	0.19
lvs only hirsute	-0.004	0.07	0.04
stms only hirsute	-0.14	-0.05	0.01
lvs & stms glabrous	-0.02	0.08	0.02
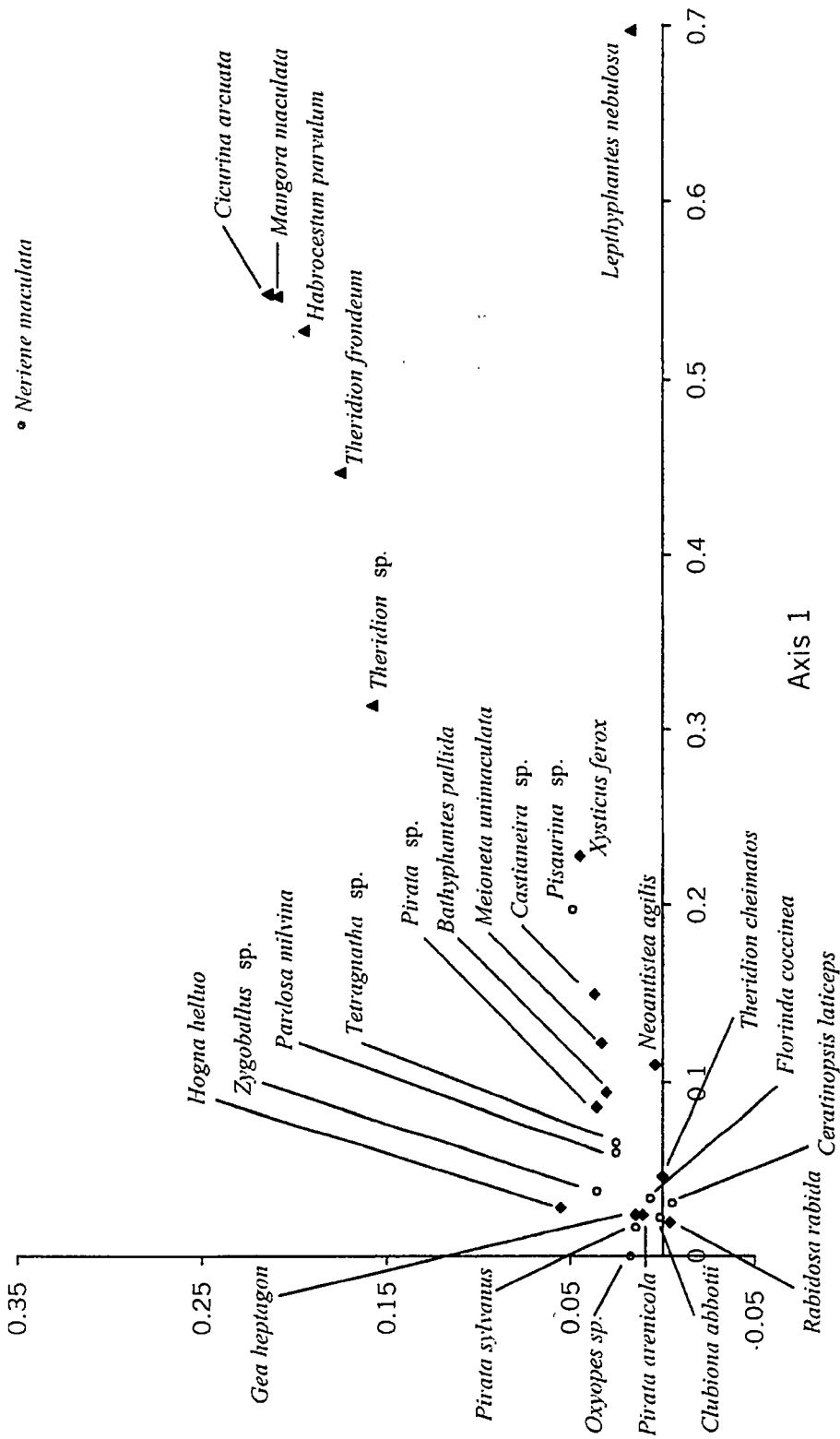
Figure 7. Bray-Curtis ordination of transposed spider species matrix (i.e., ordination of species in quadrat space). Diamonds = species found primarily in the SF, circles = TGF, and triangles = DW. Three species (*Hogna helluo* [Lycosidae], *Oxyopes* sp. [Oxyopidae], and *Theridion cheimatos* [Theridiidae] were found in nearly equal proportions in the sloped field and tussock grass field.

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clearest separation from other species. Separation of species found primarily in either the sloped field (diamonds) or tussock grass field (open circles) is indistinct. Three of the species (*Hogna helluo* [Lycosidae], *Oxyopes* sp. [Oxyopidae], and *Theridion cheimatos* [Theridiidae]) were present in comparable numbers in these two sites. Of the 17 remaining species, the abundances of six species present in both sites were within ten percentage points of one another; the other 11 species were more clearly primarily associated with a single site (see Appendix, Table 9).

Mantel Test

The Mantel test on the distance matrices indicates highly significant congruence among all three matrices (Table 4). The greatest association is between the plant species and spider species matrices ($r = 0.44$, $p < 0.0001$), followed by a strong association between the habitat and spider species matrices ($r = 0.37$, $p < 0.0001$). Nineteen percent (i.e., $r^2 = 0.44^2 = 0.19$) of the information about quadrats based on the spider species composition was reproduced by the composition of the plant species, while 14% (i.e., $r^2 = 0.37^2 = 0.14$) was reproduced by habitat structure/physiognomy. The plant and habitat matrices also exhibited a significant association, though only eight percent of the information in one was reproduced in the other ($r = 0.29$, $p < 0.0001$). Unfortunately, all three matrices were singular[b] and the partial correlation coefficients could not be calculated to account for covariation among the matrices. However, inspection of a graph of the plant and habitat scores from the first ordination axis plotted against the

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[b] A singular matrix is not of full rank; i.e., it does not have an inverse (Rencher 1995; Neter *et al.* 1996) and therefore correlation (and regression) analyses cannot be applied.

Table 4

Mantel Test for Association Between Distance Matrices. The Standardized Mantel Statistic (r) is a Correlation Coefficient and the Test Statistic has a t-Distribution; $t > 0$ Indicates a Positive Association

	Spider	Plant	Habitat
Spider	—		
Plant	$r = 0.44$ $t = 12.08$ $p < 0.0001$	—	
Habitat	$r = 0.37$ $t = 10.36$ $p < 0.0001$	$r = 0.29$ $t = 10.03$ $p < 0.0001$	—

scores of the first spider ordination axis clearly shows a stronger relationship between the plant and spider species compositions ($R = 0.72$) compared to the relationship between spider species composition and habitat ($R = 0.44$) (Figure 8). A somewhat weaker relationship is evident between plant species composition and habitat ($R = 0.32$) (Figure 9).

Regression Analyses

The stepwise variable selection algorithm available in SAS's PROC REG and PROC LOGISTIC was employed to build regression models. Stepwise selection begins with the intercept as the only parameter in the model. Variables are added based on the significance they contribute to the model, and at each step the entire model is evaluated, and variables not meeting the chosen alpha are removed. In this way relationships between independent variables can be accounted for in the regression model.

The user controls the criteria for entry into the model and removal from the model. The significance for entry was set at 0.70 to allow as many variables as possible into the model for testing. The removal criterion was ostensibly a significance value of 0.05. However, the actual removal criterion was considerably more stringent because numerous regressions were being performed. To maintain a constant alpha while performing several regressions, the Bonferroni correction was used on subsets of the dependent variables. Five abundance/diversity measures were used as dependent variables in the multiple regressions (number of spiders per quadrat, number of species per quadrat, spider diversity [H'], spider evenness [$E_{H'}$], and number of guilds per quadrat), and therefore 0.05 was divided by 5 and the actual removal criterion was set at
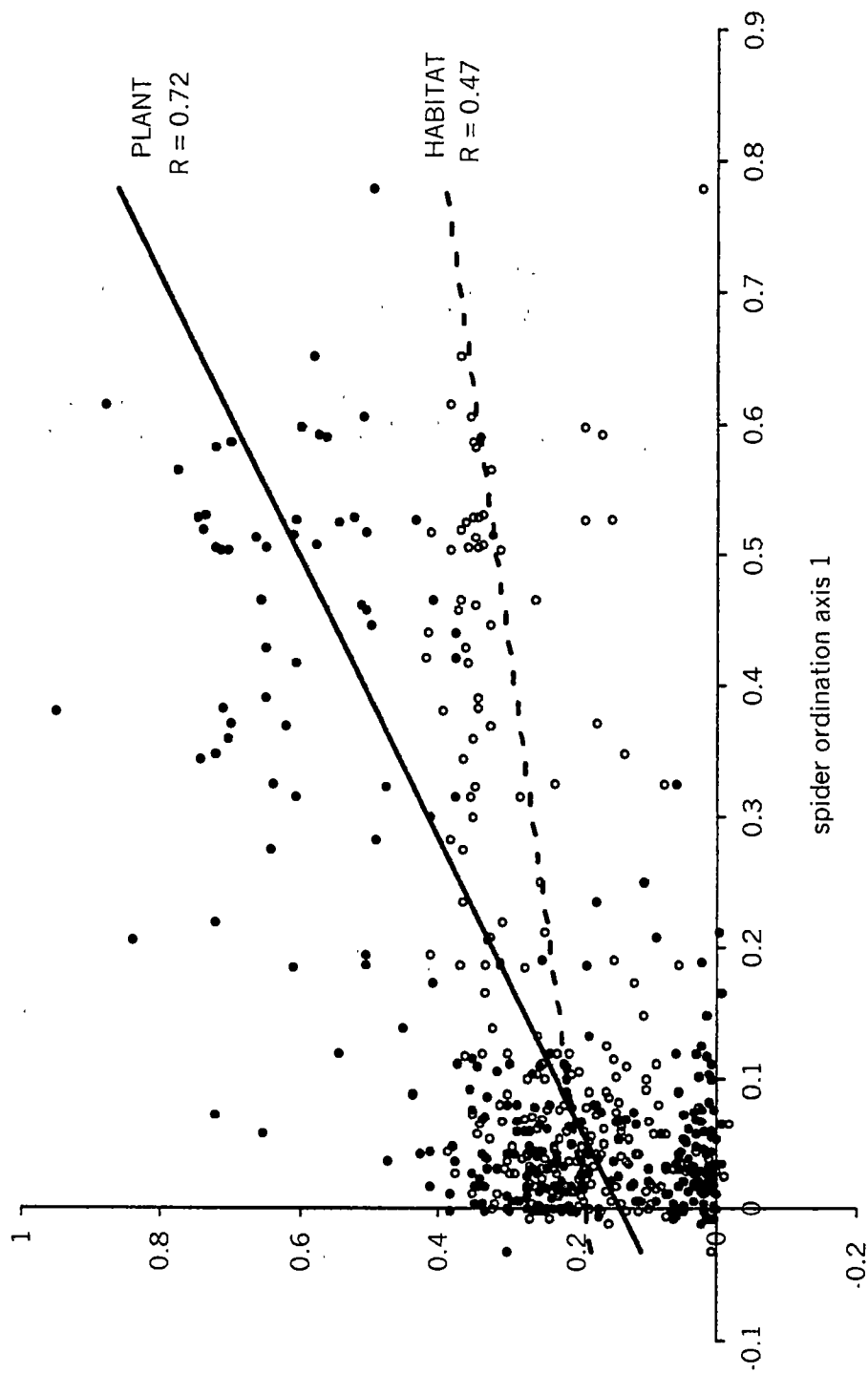
Figure 8. Correlations between first axis of Bray-Curtis ordination of spider species with first axes from ordinations of plant species and habitat variables. Closed circles represent coordinates from plant species ordination; open circles represent coordinates from habitat variable ordination.
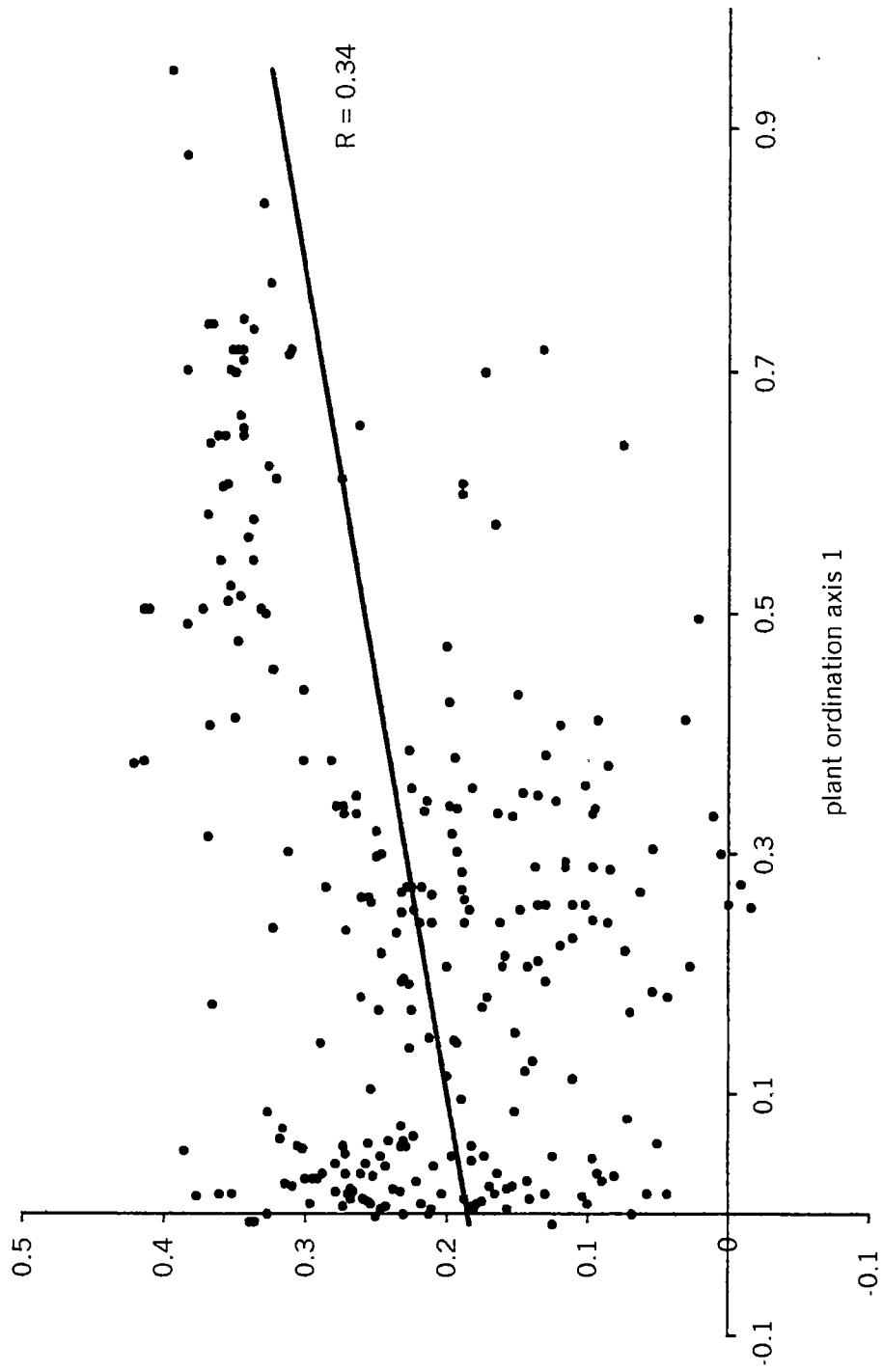
Figure 9. Correlation between first axis of Bray-Curtis ordination of plant species with first axis from ordination of habitat variables.

0.01. Logistic regressions were performed on twelve individual spider species, resulting in a removal criterion of 0.0042 (0.05/12). Data from the different sampling periods and sites were pooled based on the lack of evidence of significant variation among sampling periods (Figures 4, 5, and 6), and the fact that the ordination scores reflected those differences existing among the three sites.

Habitat configuration was the only significant predictor of the abundance and diversity variables in the linear regressions (Table 5). Three of the dependent variables, number of species and guilds per quadrat and spider diversity, were predicted by habitat ordination axis 1, which exhibited a strong negative correlation with vegetation density (Table 3). The number of spiders per quadrat was predicted by habitat ordination axes 2 and 3, which were strongly positively correlated with mean vegetation height (habitat ordination axis 2 [Table 3]) and with both vegetation density and the standard deviation of vegetation height (habitat ordination axis 3 [Table 3]).

Individual spider species exhibited different responses to the independent variables tested here (Table 6). Three of the twelve species were predicted by habitat configurations (habitat ordination axis 1, negatively correlated with vegetation density): the sheet line weaver *Bathyphantes pallida* (Linyphiidae), the diurnal hunting spider *Pirata* sp. (Lycosidae), and the scattered line weaver *Theridion cheimatos* (Theridiidae). Three species representing three guilds (*Castianeira* sp. [Clubionidae], *Meioneta unimaculata* [Linyphiidae], and *Pisaurina* sp. [Pisauridae]) had no significant predictors and did not appear to discriminate among quadrats based on habitat configuration or plant species assemblages. The remaining six species, representing four guilds, were associated with plant ordination axis 1 and/or 2. *Pardosa milvina* (Lycosidae), *Pirata*

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Table 5

Regression Statistics for Linear Regressions*

Dependent Variable	Independent Variable	p-value	F Statistics	R^2
NUMBER OF INDIVIDUALS	habitat ordination axis 3**	< 0.0001	F = 13.07	0.09
	habitat ordination axis 2	0.01	$p < 0.0001$	
NUMBER OF SPECIES	habitat ordination axis 1	0.0001	F = 15.40 $p = 0.0001$	0.06
NUMBER OF GUILDS	habitat ordination axis 1	0.004	F = 8.58 $p = 0.004$	0.03
SPIDER DIVERSITY (H')	habitat ordination axis 1	0.005	F = 8.07 $p = 0.005$	0.03
SPIDER EVENNESS ($E_{H'}$)	no significant predictor			

*Detailed regression statistics are given in the Appendix, Table 10.
** The habitat ordination axes exhibited the strongest correlations (Table 3) with:
        vegetation density (negative correlation, axis 1),
        mean vegetation height (positive correlation, axis 2), and
        vegetation density and standard deviation of veg. height (positive correlations, axis 3).

Table 6

Regression Statistics for Logistic Regressions*

Guild **	Dependent Variable	Independent Variable	p-value	Likelihood Ratio	$\tilde{R}^{2\dagger}$
Nocturnal hunting spiders	*Castianeira* sp. (Clubionidae)	no significant predictor			
Sheet line weavers	*Bathyphantes pallida* (Linyphiidae)	habitat ord. axis 1[††]	.0005	$\chi^2 = 12.63$ $p = 0.0005$	0.07
	Meioneta unimaculata (Linyphiidae)	no significant predictor			
Diurnal hunting spiders	*Pardosa milvina* (Lycosidae)	plant ord. axis 1	< 0.0001	$\chi^2 = 23.72$ $p < 0.0001$	0.11
	Pirata sylvanus (Lycosidae)	plant ord. axis 1	0.0005	$\chi^2 = 15.58$ $p < 0.0001$	0.09
	Pirata sp. (Lycosidae)	habitat ord. axis 1	< 0.0001	$\chi^2 = 23.56$ $p < 0.0001$	0.11
	Oxyopes sp. (Oxyopidae)	plant ord. axis 1	< 0.0001	$\chi^2 = 22.12$ $p < 0.0001$	0.12
	Pisaurina sp. (Pisauridae)	no significant predictor			
Orb weavers	*Tetragnatha* sp. (Tetragnathidae)	plant ord. axis 1	< 0.0001	$\chi^2 = 22.98$ $p < 0.0001$	0.18
Scattered line weavers	*Theridion cheimatos* (Theridiidae)	habitat ord. axis 1	0.0002	$\chi^2 = 14.98$ $p = 0.0001$	0.08
	Theridion frondeum (Theridiidae)	plant ord. axis 1	< 0.0001	$\chi^2 = 73.00$ $p < 0.0001$	0.37
		plant ord. axis 2	0.008		
Crab spiders	*Xysticus ferox* (Thomisidae)	plant ord. axis 2	0.005	$\chi^2 = 8.57$ $p = 0.003$	0.06

* Detailed regression statistics are given in the Appendix, Table 11.

** Guild delineations from Post and Riechert (1977).

[†] $\tilde{R}^2$ = Max-Rescaled R^2; proposed by Nagelkerke (1991) because in logistic regression the maximum value that R^2 can take is not always 1, as it is in least-squares regression.(Nagelkerke 1991, SAS Institute Inc.).

[††] See note (**), Table 5, for variables strongly correlated with habitat ordination axes.

sylvanus (Lycosidae), *Oxyopes* sp. (Oxyopidae), and *Tetragnatha* sp. (Tetragnathidae) were associated with plant ordination axis 1. *Theridion frondeum* (Theridiidae) was predicted by plant ordination axes 1 and 2, and *Xysticus ferox* (Thomisidae) was predicted by plant ordination axis 2. Detailed regression statistics for both linear and logistic models are presented in the Appendix (Tables 10 and 11), as well as regression statistics for models built without employing the Bonferroni correction (Tables 12 and 13).

IV. DISCUSSION

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Any interpretations of the results from the analyses reported in this study could be confounded by the different sample sizes in 1997 and 1998. In the preliminary year of data collection a fixed number of quadrats (20) were sampled in each site in July and again in September. The following year, adequate sample size was determined using the method of Post and Riechert (1977) described here in the sampling methods. As a result more quadrats were sampled in the sloped field and tussock grass fields than in the first year, though the number of quadrats in the deciduous woodland was unchanged. Sample sizes from the first year may not have been adequate to accurately reflect the spider communities in the former sites. However, no clear pattern reflecting inadequate sample sizes in year one was detected in the basic sampling statistics (Table 1). In the tussock grass field, for example, the mean number of individuals per quadrat was actually lower in the second year, and the coefficient of variation somewhat higher. In any event, conclusions drawn from the 1997 sampling season for the two field sites should be made with caution.

Descriptive Statistics

Diversity

Although the sloped field had the greatest mean species richness (S) of the three habitats, followed by the tussock grass field and the deciduous woodland, it had the lowest mean value of the Shannon-Wiener diversity index (H'). Remarkably, the

deciduous woodland had the highest diversity based on this index, despite the fact that it had 25% fewer species than the sloped field. The Shannon-Wiener index incorporates the two primary components of diversity: richness and evenness. The high evenness or equitability found in the deciduous woodland indicates that it is this component of diversity that explains the pattern demonstrated by the Shannon-Wiener values.

The deciduous woodland also exhibited the least variation among sampling periods in terms of richness, diversity, and evenness. This habitat experiences the least temporal variation of the three; both the sloped field and tussock grass field are composed of a number of fast growing plant species, and consequently there is considerable seasonal change in habitat architecture in these two sites. Additionally, the deciduous woodland supports fewer herbaceous and grass species, as well as fewer plant individuals. As a result the deciduous woodland is a more homogeneous and less structurally complex habitat from the perspective of the spider community (which is dominated in this site by ground-running and litter spiders), relative to the sloped and tussock grass fields. This comparative temporal and spatial uniformity may foster a certain uniformity within the spider community as well, or perhaps *limit* the diversity of the spider community.

<center>Habitat Associations</center>

Ordination Analyses

Although the habitat ordination (Figures 4-6) explained more of the variance among quadrats than did the plant species ordination (Figure 2) (97.37% for the habitat

ordination compared with 68.72% for the plant species ordination), the three sites are much more clearly distinguished on the basis of plant species composition. It appears that while the endpoint quadrats for each axis in the habitat ordination are more dissimilar than are the endpoint quadrats in the plant species ordination, the remaining quadrats are more evenly spaced along each axis when habitat variables are being considered. This implies that there is a comparative continuum of configurations of habitat variables among quadrats in the different sites, while plant species assemblages are generally more discrete. The ordination of quadrats based on spider species (Figure 3) explained only 46.05% of the variance, but as in the habitat ordination the spider species assemblages did not clearly separate the sites; again, there appears to be a continuum of spider species assemblages. In both the habitat and spider species ordinations, this continuum is most evident between the sloped and tussock grass fields with lesser degrees of overlap with the deciduous woodland.

The ordination of the transposed matrix of spider species illustrates species positions in the ordination space based on the quadrats in which they occurred (Figure 7). Here, rather than being based on species composition the ordination is based on "quadrat composition." Species occurring primarily in the deciduous woodland (triangles in Fig. 7) were distinct from those occurring primarily in either the sloped field or tussock grass field. Species occurring primarily in the latter two sites, however, showed no clear separation. As in the ordinations of quadrats based on spider species and habitat variables, the deciduous woodland was the only distinguishable site, lending further support to the idea of a continuum between the sloped field and tussock grass field.

Mantel Test

There was significant correspondence between each of the three distance matrices, the highest being between the plant and spider species matrices. The significant association between the plant and habitat matrices, while weaker than the other comparisons, may confound interpretations of their respective interactions with members of the spider community. Rotenberry (1985) addressed this problem with partial correlations of his bird, plant, and habitat matrices to control for the covariation of the matrices under consideration in the correlation with a third matrix. This solution was not an option here, as the correlation matrices were singular. There is other evidence, though, to support the conclusion that the plants and spiders are more closely related than are the spiders and habitat variables. A look at Figure 8, comparing the association between the first axis of the spider ordination with the first axes of both the plant and habitat ordinations, illustrates that the plant axis captures 51% (i.e., $r^2 = 0.72^2 = 0.51$) of the variation in the spider axis while the habitat axis captures only 22% (i.e., $r^2 = 0.47^2 = 0.22$).

Regression Analyses

Results from the regression analyses confirm the conclusions from previous studies regarding the differences in the sensitivity or responses of different spider species to features of their environment. The distributions of the species under investigation here were predicted by different independent variables, plant species assemblages and habitat. Three of the species' distributions showed no relationship with these variables. Given our

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understanding of the ways in which species coexistence may be facilitated by the partitioning of habitat (i.e., niche partitioning), it is certainly reasonable to expect that species in a community will exhibit dissimilar associations with their habitat, both in the features to which they respond and the degree to which they respond to any given characteristic. Some may be specialized in their use of some aspect of habitat space while others may be generalists, and these roles are to some extent dependent on the resource gradient in question.

These results also provide somewhat surprising evidence, supported by the results of the Mantel test, that the plant species themselves are quite important in the organization of spider communities. This runs counter to our intuition; spiders are not phytophagous, and previous work has indicated that for web attachment sites and retreats spiders do not discriminate between natural and artificial substrates (Bultman &Uetz 1982; T. Jones, pers. comm.). The plant species ordination demonstrated a clear separation of sites (Figure 2) and separating the roles of site and plant species in determining spider species distributions may be difficult. Spider species occurring primarily within a given site may be associating with some aspect of the plant species themselves, or they (as well as the plants) may be responding to some other feature unique to that site such as surface temperature of the substrate, moisture availability, or prey composition and abundance.

A caveat about the regression analyses and subsequent conclusions is warranted. As Rotenberry (1985) points out regarding the use of correlations to compare distance matrices, traditional statistical tests of significance are of limited utility when the variables themselves are not independent. The independence of ordination scores on an

axis is questionable, given that these values are derived from a distance matrix; therefore the interpretation of p-values from the application of regression analyses may not be entirely reliable. However, the results of the regressions were in accord with the results of the Mantel test. Bearing that in mind, even the provisional conclusions based on these analyses point to some very interesting research questions and future directions. Furthermore, spider species interactions with one another play an important role in shaping spider communities; these interactions are being investigated in work not presented here.

Conclusions

These results suggest that spider species are responding to plant species assemblages to a greater extent than to habitat factors. This contradicts the evidence in spider ecology literature (for examples see Hatley & MacMahon 1980; Robinson 1981; Abraham 1983; Uetz 1991; Wise 1993; Balfour & Rypstra 1998). I suggest two possible, non-exclusive explanations for this discrepancy. First, researchers have had very little reason to think that spiders would associate with specific plant species, as they do not rely on plant products (fruits, flowers) themselves, and they are generalist predators (i.e., they wouldn't be expected to associate with plant species based on the prey attracted by that plant). None of the studies mentioned above included information about the plant species composition itself in the communities being studied. Therefore the lack of evidence for (or against) an association between plant species and spider species is a result of the association not being examined, rather than a failure of detection.

Second, I believe it is unlikely that spiders are truly responding to plant species per se. Rather, I would argue that, though the measurements of habitat structure employed here did correspond to patterns of spider abundance and diversity, they were too coarse to capture the features to which individual spider species do respond. The plant species themselves may do a better job of measuring or representing the structural or physiognomic attributes at the fine scale that is meaningful to a spider. This issue can only be addressed through further investigation of these communities manipulating habitat structure and plant species in both lab and field experiments.

Conclusions from the current study are also somewhat limited by the nature of the data themselves. The lack of independence among the values of observations for each ordination axis restricts the application of traditional statistical tests to these data. Standard correlations between axes can be interpreted qualitatively only; p-values may not be accurate. Similarly, the axes may not be appropriate for use in regression analyses because they violate the assumption of independence of the observations. However, our inability to apply robust statistical tests to, and therefore draw sound conclusions about, data in which a pattern is evident is insufficient reason to dismiss the pattern entirely. Rather, data such as these should be seen as laying the groundwork for future research in which a) experiments are designed in such a way as to produce data that are amenable to standard statistical testing, or b) experiments are designed to answer questions conceived and posed within the framework of nontraditional statistical approaches, such as Bayesian inference and information theory.

Summary

I posed three questions at the outset of this study that I will address in summary.

Q1: Are the three sites distinguishable on the basis of unique habitat configurations or plant species assemblages? Plant species assemblages were the most effective in providing clear delineations among quadrats within each of the three sites. In the spider species ordination the two field sites (sloped and tussock grass fields) were indistinguishable, while the deciduous woodland site was somewhat separated. The ordination of the habitat variables demonstrated even less separation, though as in the spider species ordination the woodland quadrats exhibited the greatest (albeit small) differentiation relative to the other sites

Q2: How and to what extent are the spider communities of these three sites influenced by unique habitat configurations or plant species assemblages? The spider community as a whole was significantly associated with both plant assemblages and habitat configurations. Spider abundance and diversity were significantly predicted by aspects of habitat only, but the spider species assemblages were most closely associated with the plants, with a slightly weaker association with the habitat ordination.

Q3: How do individual spider species respond to habitat and plant species assemblages? Individual species exhibited a variety of responses to the variables measured in this study. Three species of the twelve analyzed were associated with habitat. Another three species showed no associations at all. The remaining six species were all significantly associated with plant species assemblages; as mentioned above, this variable is very closely associated with site and the two are not easily distinguishable in their relative effects on spider species.

Previous work has indicated that habitat structure is a significant element in organizing a variety of animal communities. Researchers have demonstrated this quite successfully for spider communities as well. The current work has yielded potentially contradictory evidence regarding the role of habitat structure in spider communities. Further research is needed to investigate the scale at which spiders respond to their physical surroundings, as well as to incorporate information not gathered in this study: prey availability and its relation to plant physiognomy and floristics, details of microclimate, and experimental manipulations designed to investigate spider species interactions with one another.

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APPENDICES

Table 7

Species List of Spiders, Grouped by Family. Presence in Each Site is Indicated by an "x."

Spider Species	Sloped Field	Tussock Grass Field	Deciduous Woodland
Agelenidae			
Cicurina arcuata	x	x	x
Wadotes sp.			x
Amaurobiidae			
Amaurobius sp.		x	
Antrodiaetidae			
Antrodiaetus unicolor			x
Anyphaenidae			
Anyphaena pectorosa	x	x	x
Araneidae			
Acanthepeira sp.	x	x	x
Araneus sp.	x		
Argiope aurantia		x	
Argiope trifasciata	x	x	
Gea heptagon	x	x	
Mangora maculata			x
Neoscona hentzii			x
Nuctenea sp.			x
Verrucosa arenata			x
Clubionidae			
Castianeira sp.	x	x	x
Chiracanthium sp.			x
Clubiona abbotii	x	x	
Clubionoides sp.		x	x
Phrurolithus fratrellus		x	x
Phrurotimpus alarius			x
P. borealis			x
Trachelas similis			x
Gnaphosidae			
Drassylus eremitus	x	x	
Hahniidae			
Neoantistea agilis	x		x
Leptonetidae			
Leptoneta gertschi			x
Linyphiidae			
Bathyphantes pallida	x	x	x
Ceraticelus fissiceps	x		
C. laetabilis			x
Ceratinopsis laticeps	x	x	
Ceratinopsis sp.	x	x	
Eperigone maculata			x
Eridantes erigonoides	x		
Florinda coccinea	x	x	x
Frontinella communis	x	x	

Table 7 (continued)

Spider Species	Sloped Field	Tussock Grass Field	Deciduous Woodland
(Linyphiidae, cont.)			
Grammonota ornata		x	
G. pictilis			x
Graphomoa theridioides		x	
Islandia flaveola			x
Lepthyphantes nebulosa			x
Meioneta longipes	x		
Meioneta micaria		x	x
Meioneta picta	x		
M. unimaculata	x	x	x
M. zygia		x	x
Microneta viaria	x		
Microneta sp.		x	
Neriene clathrata	x	x	x
N. maculata	x	x	x
Origanates rostratus	x		x
Walckenaeria spiralis	x	x	
species E (Erigoninae)			x
Lycosidae			
Allocosa funerea	x		
Hogna helluo	x	x	
Pardosa milvina	x	x	x
Pirata arenicola	x	x	
P. insularis		x	
P. sylvanus	x	x	x
Pirata sp.	x	x	x
Rabidosa rabida	x	x	
Schizocosa crassipes	x		
Trabea aurantiaca	x	x	
Mimetidae			
Ero pensacolae	x		
Oxyopidae			
Oxyopes sp.	x	x	
Philodromidae			
Philodromus sp.			x
Pisauridae			
Pisaurina undulata			
Pisaurina sp.	x	x	x
Salticidae			
Ballus sp.	x		
Eris militaris	x	x	x
Habrocestum parvulum	x	x	x
Habronattus coronatus	x		
Maevia sp.	x	x	x
Marpissa lineata	x	x	
Phiddipus sp.		x	
Sitticus floridanus	x		

Table 7 (continued)

Spider Species	Sloped Field	Tussock Grass Field	Deciduous Woodland
(Salticidae, cont.)			
Thiodina sylvana	X	X	
Zygoballus bettini	X		
Zygoballus nervosus	X	X	
Zygoballus sp.	X	X	
Tetragnathidae			
Leucauge venusta			X
Pachygnatha autumnalis	X	X	X
Tetragnatha sp.	X	X	X
Theridiidae			
Euryopis funebris		X	X
Robertus sp.		X	X
Theridion albidum	X	X	X
T. cheimatos	X	X	X
T. frondeum	X	X	X
T. neshamini	X		
Theridion sp.	X	X	X
Theridula opulenta	X	X	X
Thomisidae			
Misumena vatia		X	
Misumenoides formosipes		X	
Misumenops sp.	X	X	
Ozyptila monroensis			X
Synema sp.	X		X
Tmarus sp.			X
Xysticus ferox	X	X	X
Zoridae			
Zora pumilis	X		

Table 8

List of Plant Species. Presence in Each Site is
Indicated by an "x."

Plant Species	Sloped Field	Tussock Grass Field	Deciduous Woodland
Acer negundo		x	x
Acer sp.			x
Albizia julibrissin	x		
Ambrosia artemisiifolia	x		
Amphicarpaea bracteata		x	x
Ampelopsis cordata		x	x
Ambrosia trifida	x		
Apios americana		x	
Apocynum cannabinum		x	
Arisaema triphyllum			x
Asplenium platyneuron			x
Bignonia capreolata			x
Boehmeria cylindrica	x	x	
Carya cordiformis			x
Campsis radicans	x	x	
Carex sp.		x	
Cerastium vulgatum	x		
Cimicifuga racemosa			x
Convulvulus arvensis	x	x	
Conopholis sp.			x
Dactylis glomerata	x		
Dentaria laciniata			x
Desmodium sp.	x	x	
Diodia virginiana	x	x	
Dioscorea villosa	x	x	
Euonymus sp.			x
Festuca sp.		x	
Geum canadense			x
Glechoma hederacea	x	x	
Impatiens capensis		x	
Ipomea sp.		x	
Juglans nigra			x
Lespedeza cuneata	x	x	
Leersia sp.		x	
Lindera benzoin			x
Lonicera dioica	x	x	x
Lonicera japonica	x		x
Lysimachia nummularia	x	x	
Menispermum canadense	x		x
Melothria pendula	x		
Mitchella repens			x

Table 8 (continued)

Plant Species	Sloped Field	Tussock Grass Field	Deciduous Woodland
Microstegium vimineum	X	X	X
Oxalis sp.	X		
Parthenocissus quinquefolia	X		X
Panicum sp.		X	
Physalis sp.	X		
Pilea pumila			X
Plantago sp.	X		
Polystichum acrostichoides			X
Podophyllum peltatum			X
Polygonatum pubescens			X
Poa sp.	X	X	
Polygonum sp.	X	X	X
Polygonum virginianum			X
Rhus radicans	X	X	X
Ruellia caroliniensis		X	
Smilacina racemosa			X
Solidago canadensis		X	
Solanum carolinense	X	X	
Trifolium sp.	X		
Ulmus rubra			X
Vernonia gigantea	X	· X	
Verbesina sp.	X		
Vicia grandiflora	X		
Vitis sp.	X	X	
Viola sp.	X	X	X
Waldsteina fragarioides	X	X	X
Lobelia?	X		
Mimosa sp.		X	
Unknown A	X		
Unknown B	X		
Unknown C	X		

Table 9

Percentage of Quadrats Within Each Site Occupied by Abundant* Spider Species

Spider Species	Sloped Field	Tussock Grass Field	Deciduous Woodland
Cicurina arcuata (Agelenidae)	0.93%	1.00%	22.50%
Gea heptagon (Araneidae)	16.67%	8.00%	absent
Mangora maculata ((Araneidae)	absent	absent	18.75%
Castianeira sp. (Clubionidae)	21.30%	7.00%	7.50%
Clubiona abbotii (Clubionidae)	33.33%	36.00%	absent
Neoantistea agilis (Hahniidae)	17.59%	absent	5.00%
Bathyphantes pallida (Linyphiidae)	41.67%	28.00%	11.25%
Ceratinopsis laticeps (Linyphiidae)	absent	14.00%	absent
Florinda coccinea (Linyphiidae)	absent	10.00%	1.25%
Lepthyphantes nebulosa (Linyphiidae)	absent	absent	26.25%
Meioneta unimaculata (Linyphiidae)	19.44%	9.00%	7.50%
Neriene maculata (Linyphiidae)	absent	3.00%	12.50%
Hogna helluo (Lycosidae)	10.19%	10.00%	absent
Pardosa milvina (Lycosidae)	37.96%	47.00%	11.25%
Pirata arenicola (Lycosidae)	15.74%	1.00%	absent
Pirata sylvanus (Lycosidae)	17.59%	23.00%	2.50%
Pirata sp. (Lycosidae)	68.52%	43.00%	20.00%
Rabidosa rabida (Lycosidae)	22.22%	2.00%	absent
Oxyopes sp. (Oxyopidae)	24.07%	26.00%	absent
Pisaurina sp. (Pisauridae)	7.41%	17.00%	11.25%
Habrocestum parvulum (Salticidae)	4.63%	1.00%	26.25%
Zygoballus sp. (Salticidae)	8.33%	12.00%	absent
Tetragnatha sp. (Tetragnathidae)	6.48%	25.00%	2.50%
Theridion cheimatos (Theridiidae)	45.37%	41.00%	6.25%
Theridion frondeum (Theridiidae)	3.70%	7.00%	52.50%
Theridion sp. (Theridiidae)	2.78%	4.00%	11.25%
Xysticus ferox (Thomisidae)	18.52%	3.00%	12.50%

* i.e., species present in   5% of the total number of quadrats.

Table 10

Parameter Estimates and Complete Regression Statistics for
Linear Regressions.

Dependent Variables	Independent Variable	df	Parameter Estimate	p-value	Regression Statistics		
					F	p	R^2
NUMBER OF INDIVIDUALS	intercept	1	-1.27	0.52			
($n = 266$)	habitat ordination axis 3	1	32.34	<.0001	13.07	<.0001	0.09
	habitat ordination axis 2	1	11.02	0.01			
NUMBER OF SPECIES	intercept	1	6.30	<.0001			
($n = 266$)	habitat ordination axis 1	1	-6.33	0.0001	15.40	0.0001	0.06
NUMBER OF GUILDS	intercept	1	3.96	< 0.0001			
($n = 266$)	habitat ordination axis 1	1	-2.61	0.004	8.58	0.004	0.03
H' (SPIDER RICHNESS)	intercept	1	1.54	<.0001			
($n = 261$)	habitat ordination axis 1	1	-0.97	0.005	8.07	0.005	0.03
E_H (SPIDER EVENNESS)	no significant predictors						

Table 11

Parameter Estimates and Complete Regression Statistics for Logistic Regressions

Dependent Variable	Independent Variable	df	Parameter Estimate	p-value	Odds Ratio	Goodness of Fit (Hosmer-Lemeshow) χ^2	p	Regression Statistics Likelihood Ratio (χ^2)	p	$\bar{R}^2$
Castianeira sp. (Clubionidae)	no significant predictors									
Bathyphantes pallida (Linyphiidae) (*n* = 288)	intercept	1	0.22	0.50		9.40	0.31	12.63	0.0004	0.07
	habitat ord. axis 1	1	-4.83	0.0005	0.008					
Meioneta unimaculata (Linyphiidae)	no significant predictors									
Pardosa milvina (Lycosidae) (*n* = 288)	intercept	1	0.06	0.74		6.85	0.55	23.72	<.0001	0.11
	plant ord. axis 1	1	-2.81	<.0001	0.06					
Pirata sylvanus (Lycosidae) (*n* = 288)	intercept	1	-0.98	<.0001		13.27	0.10	15.58	<.0001	0.09
	plant ord. axis 1	1	-3.21	0.0005	0.04					

Table 11 (continued)

Dependent Variable	Independent Variable	df	Parameter Estimate	p-value	Odds Ratio	Goodness of Fit (Hosmer-Lemeshow)		Regression Statistics		
						χ^2	p	Likelihood Ratio (χ^2)	p	$\bar{R}^2$
Pirata sp. (Lycosidae) (*n* = 288)	intercept	1	1.38	< 0.0001						
	habitat ord. axis 1	1	-6.32	<.0001	0.002	18.48	0.02	23.56	<.0001	0.11
Oxyopes sp. (Oxyopidae) (*n* = 288)	intercept	1	-0.69	0.002						
	plant ord. axis 1	1	-3.66	< 0.0001	0.03	9.81	0.28	22.12	<.0001	0.12
Pisaurina sp. (Pisauridae)	no significant predictors									
Tetragnatha sp. (Tetragnathidae) (*n* = 288)	intercept	1	-0.96	<.0001						
	plant ord. axis 1	1	-5.64	< 0.0001	0.004	8.77	0.36	22.98	<.0001	0.18
Theridion cheinatos (Theridiidae) (*n* = 288)	intercept	1	0.51	0.11						
	habitat ord. axis 1	1	-5.11	0.0002	0.006	24.66	0.0002	14.98	0.0001	0.08

Table 11 (continued)

Dependent Variable	Independent Variable	df	Parameter Estimate	p-value	Odds Ratio	Goodness of Fit (Hosmer-Lemeshow) χ^2	p	Regression Statistics Likelihood Ratio (χ^2)	p	R^2
Theridion frondeum (Theridiidae) (n = 288)	intercept	1	-4.28	<.0001						
	plant ord. axis 1	1	5.26	< 0.0001	192.16	7.13	0.52	73.00	<.0001	0.37
	plant ord. axis 2	1	2.89	0.008	18.03					
Xysticus ferox (Thomisidae) (*n* = 288)	intercept	1	-1.27	<.0001						
	plant ord. axis 2	1	-2.84	0.005	0.06	2.06	0.98	8.57	0.003	0.06

Table 12

Parameter Estimates and Complete Regression Statistics for Linear
Regression Models without Bonferroni Correction.

Dependent Variables	Independent Variable	df	Parameter Estimate	p-value	Regression Statistics		
					F	p	R^2
NUMBER OF INDIVIDUALS	intercept	1	3.46	0.17			
($n = 266$)	habitat ordination axis 3	1	26.35	0.0003			
	habitat ordination axis 2	1	10.29	0.02	12.81	<.0001	0.13
	habitat ordination axis 1	1	-13.70	0.0003			
NUMBER OF SPECIES	intercept	1	3.91	<.0001			
($n = 266$)	habitat ordination axis 3	1	5.94	0.03			
	habitat ordination axis 2	1	3.49	0.03	8.11	<.0001	0.09
	habitat ordination axis 1	1	-4.94	0.004			
NUMBER OF GUILDS	intercept	1	3.96	< 0.0001			
($n = 266$)	habitat ordination axis 1	1	-2.61	0.004	8.58	0.004	0.03
H^i (SPIDER RICHNESS)	intercept	1	1.54	<.0001			
($n = 261$)	habitat ordination axis 1	1	-0.97	0.005	8.07	0.005	0.03
E_{11} (SPIDER EVENNESS)	no significant predictors						

Table 13

Parameter Estimates and Complete Regression Statistics for Logistic Regression Models without Bonferroni Correction.

Dependent Variable	Independent Variable	df	Parameter Estimate	p-value	Odds Ratio	Goodness of Fit (Hosmer-Lemeshow)		Regression Statistics		
						χ^2	p	Likelihood Ratio (χ^2)	p	$\bar{R}^2$
Castianeira sp. (Clubionidae) ($n = 288$)	intercept	1	-1.28	< 0.0001		6.61	0.58	7.15	0.0008	0.05
	plant ord. axis 2	1	-2.51	0.009	0.082					
Bathyphantes pallida (Linyphiidae) ($n = 288$)	intercept	1	0.22	0.50		9.40	0.31	12.63	0.0004	0.07
	habitat ord. axis 1	1	-4.83	0.0005	0.008					
Meioneta unimaculata (Linyphiidae) ($n = 288$)	intercept	1	-0.87	0.03		12.83	0.12	7.61	0.006	0.05
	habitat ord. axis 1	1	-5.09	0.007	0.006					
Pardosa milvina (Lycosidae) ($n = 288$)	intercept	1	0.06	0.74		6.85	0.55	23.72	<.0001	0.11
	plant ord. axis 1	1	-2.81	<.0001	0.06					

Table 13 (continued)

Dependent Variable	Independent Variable	df	Parameter Estimate	p-value	Odds Ratio	Goodness of Fit (Hosmer-Leneshow)		Regression Statistics		
						χ^2	p	Likelihood Ratio (χ^2)	p	$\bar{R}^2$
Pirata sylvanus (Lycosidae) (n = 288)	intercept	1	1.38	< 0.0001		18.48	0.02	23.56	<.0001	0.11
	plant ord. axis 1	1	-6.32	<.0001	0.002					
Pirata sp. (Lycosidae) (n = 288)	intercept	1	1.92	<.0001		8.60	0.38	34.16	<.0001	0.16
	plant ord. axis 1	1	-1.60	0.03	0.20					
	plant ord. axis 2	1	-2.45	0.002	0.09					
	habitat ord. axis 1	1	-3.77	0.02	0.02					
Oxyopes sp. (Oxyopidae) (n = 288)	intercept	1	1.10	0.13		6.13	0.63	32.90	<.0001	0.18
	plant ord. axis 1	1	-7.42	0.0006	< 0.01					
	plant ord. axis 2	1	-3.87	0.006	0.02					
Pisaurina sp. (Pisauridae)	no significant predictors									

Table 13 (continued)

Dependent Variable	Independent Variable	df	Parameter Estimate	p-value	Odds Ratio	Goodness of Fit (Hosmer-Lemeshow) χ^2	p	Regression Statistics Likelihood Ratio (χ^2)	p	$\bar{R}^2$
Tetragnatha sp. (Tetragnathidae) (*n* = 288)	intercept	1	-2.73	0.0002						
	plant ord. axis 1	1	-5.08	0.0004	0.006	4.84	0.77	31.34	<.0001	0.21
	habitat ord. axis 2	1	6.04	0.009	421.88					
Theridion cheimatos (Theridiidae) (*n* = 288)	intercept	1	0.98	0.009						
	plant ord. axis 1	1	-3.84	< 0.0001	0.02	13.48	0.10	32.18	<.0001	0.15
	plant ord. axis 2	1	-2.55	0.001	0.08					
Theridion frondeum (Theridiidae) (n = 288)	intercept	1	-4.28	<.0001						
	plant ord. axis 1	1	5.26	< 0.0001	192.16	7.13	0.52	73.00	<.0001	0.37
	plant ord. axis 2	1	2.89	0.008	18.03					

Table 13 (continued)

Dependent Variable	Independent Variable	df	Parameter Estimate	p-value	Odds Ratio	Goodness of Fit (Hosmer-Lemeshow)		Regression Statistics		
						χ^2	p	Likelihood Ratio (χ^2)	p	$\bar{R}^2$
Xysticus ferox (Thomisidae) (*n* = 288)	intercept	1	-0.15	0.81						
	plant ord. axis 2	1	-3.61	0.002	0.03	12.23	0.14	13.67	0.001	0.10
	habitat ord. axis 2	1	-4.27	0.05	0.01					

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VITA

Monica Lynn Beals was born in Madison, Wisconsin on September 24th, 1970. She spent much time during her youth on field trips with her father (a professor of Botany and Zoology at the University of Wisconsin, Madison) and his graduate students, which instilled a lifelong curiosity about the natural world. She began her schooling at Dudgeon Pre-School and Kindergarten, and attended Midvale Elementary School. After one year at Van Hise Middle School in Madison she attended the Black Earth Junior High in Black Earth, Wisconsin. She graduated from Scattergood Friends School, a four-year Quaker preparatory school in West Branch, Iowa, in 1988. That fall she entered Earlham College in Richmond, Indiana where she initially contemplated a number of different majors, and received her B.A. in Biology in 1992.

She lived in Oregon for almost four years after getting her Bachelor's degree, and in 1996 she entered the Graduate Program in Ecology and Evolutionary Biology at the University of Tennessee, Knoxville. She received her Master of Science degree in August 2001. Her doctoral work at the University of Tennessee is currently underway and partially completed, along with study for a concurrent M.S. in Statistics.