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GUILD STRUCTURE OF SPIDERS IN MAJOR CROPS

George W. Uetz: Department of Biological Sciences, University of Cincinnati, Cincinnati, Ohio 45221-0006, USA

Juraj Halaj[1] and **Alan B. Cady:** Department of Zoology, Miami University, Oxford, Ohio 45056 USA

ABSTRACT. The ecological guild concept has been of great interest to arachnologists, and the different manner in which spiders forage for a common resource—prey arthropods—has led to numerous attempts to classify them into guilds. However, questions have been raised about the validity of guilds and the taxon-centered basis of their definition. Here, we propose an alternative approach to guild classification, using quantitative analysis of ecological characteristics of spider families. While generalizations may not apply to all species within a taxon, results from this approach suggest eight major spider guilds similar to earlier guild assignments by some authors and provide a reasonable framework for future studies. We used this classification in a comparison of spider guild composition across several major crops (from published studies). While total species richness varied widely among crops, the proportion of the total species within each guild was remarkably even across crops. The relative abundance of guilds (based on numbers of individuals) varied greatly, which may reflect availability of resources within a crop type. Patterns of similarity in guild composition suggest the possibility of plant habitat structure as an influence on the spider community. Further detailed analyses of spider guilds in various crops have been constrained by both a lack of comparable quantitative data and the paucity of behavioral and natural history information available for many taxa. As recent studies have shown that assemblages of spiders can impact pest populations and reduce crop damage, a better understanding of spider guild composition and variation in spider community structure among crops is essential in future studies of the arthropod fauna in agroecosystems.

The guild concept.—The concept of the ecological guild—a group of species utilizing the same resource in similar ways—has its origins in early plant and animal ecology, when ecologists recognized the organization of trophic groups called ''Genossenschaften'' (Schimper 1903) and ''Syntrophia'' (Balogh & Loksa 1956). Modern usage of the term ''guild'' was formalized in a study of avian niche exploitation patterns as ''a group of species that exploit the same class of environmental resources in a similar way'' (Root 1967) and this concept was later extended to the arthropod fauna of collards (Root 1973). An assumption derived from competition theory is that species within guilds are most likely competitors, therefore guilds are suggested to form the basis of community organization. Since its inception, the guild concept has been applied to numerous animal and plant communities (e.g., see reviews in Hawkins & MacMahon 1989; Simberloff & Dayan 1991).

While many studies concerning guild structure of communities exist, there has been much debate over guild definitions and the circumstances under which the concept should be used. Criticisms include the lack of formal or testable definitions (Adams 1985) and misuse by investigators using taxon-centered *a priori* guild assignments (Jaksić 1981; Hawkins & MacMahon 1989; Jaksić & Medel 1990). Hawkins & MacMahon (1989) argue that while guilds constitute an ecologically appropriate context in which to study interspecific competition and complex interactions among species, most guild-centered approaches misdefine guilds, as the key element is the *resource* (e.g., ''does it matter that a particular insect species is captured by a silken spider web or a bird's beak''?) and *not* the similar manner of utilization (behavior). Simberloff & Dayan (1991) agree that taxocenes do not necessarily equal guilds, but to be properly defined, a guild must meet *both* criteria: species

[1] Current address: Department of Entomology, University of Kentucky, Lexington, Kentucky 40546-0091 USA

using the ''same class'' of resources in a behaviorally ''similar way.''

Since related species often use resources in a similar manner, guilds will reflect taxonomic relationships; distantly related taxa may not necessarily belong to the same guild, even if they use similar resources (but see Jaksić (1981)). Jaksić (1981) and Jaksić & Medel (1990) suggest there may be two types of guilds: (A) Community guilds (''true'' guilds that are syntopic, resource-based and independent of taxon or trophic level *sensu* Root (1967)); and (B) Assemblage guilds (taxon-based guilds comprising related species). These authors admonish researchers to identify the resource in question first, then construct guilds by quantitative analysis of resource acquisition.

Spider guilds.—Arachnologists have widely embraced the guild concept, as the different manners in which spiders forage for a common resource—prey arthropods—is obvious. Not surprisingly, there have been numerous attempts to classify spiders into as few as two and as many as 11 guilds, with varying degrees of specificity (Table 1). As with other taxa, problems arise assigning species to particular guilds, for generalizations based on higher taxa may not apply to all species. For example, *Castianeira* (Clubionidae) and *Sergiolus* (Gnaphosidae) are similar—diurnal, ant-mimicking species—but their families are often placed in a ''nocturnal'' guild (e.g., Post & Riechert (1977) designate these as ''nocturnal running spiders''). In addition, some taxa within a particular family (e.g., Clubionidae) may forage primarily on vegetation (e.g., *Cheiracanthium*, *Clubiona*) whereas others may be ground-dwellers (e.g., *Castianeira*, *Phrurotimpus*) (Whitcomb et al. 1963). Some members of web-building spider families such as Linyphiidae, Agelenidae and Hahniidae may move frequently and often forage off of the web, while others are sedentary. The family Lycosidae poses particular problems. For example, some lycosids are diurnal (e.g., *Schizocosa*, *Pardosa*) while others are nocturnal (e.g., *Rabidosa*). Others forage as sit-and-wait ambush predators at a burrow entrance (e.g., *Geolycosa*) while others actively move about in search of prey (e.g., *Schizocosa*, *Pardosa*). Some species, like *Hogna helluo*, actively disperse and change sites at night, but forage in a sit-and-wait manner during the day (Marshall pers. comm.). Ideally then, guild membership should reflect the natural history and behavior of single species; but such precision is not realistic as such data are presently not available for most families.

Determination of spider guilds.—Before we can attempt to define spider guilds in major agricultural crops, several key questions must be addressed: (A) Do all spiders in an agricultural field exploit the ''same class'' of resources? As spiders are generalist predators of arthropods, the argument can be made that this is true despite the diversity of trophic levels (e.g., herbivores, detritivores, parasitoids, predators) the prey represent. (B) At what level do different foraging strategies affect resource utilization and thereby constrain or subdivide the ''same class'' of resources? While at some level, nocturnal *vs.* diurnal or web-building *vs.* hunting species surely exploit different prey resources, degrees of prey specialization appear to vary widely at the species level; and data are lacking entirely for many higher taxa. Syntopic species representing different foraging strategies or distinct web structures may show great prey variability and could be considered to exploit different resource classes (Nyffeller et al. 1989). Other studies show considerable overlap in spider diets despite major differences in web structure and microhabitat use (Wise & Barata 1983; Riechert & Cady 1983). At the same time, even syntopic species exhibiting very similar foraging strategies may consume different types of prey and significantly vary in their level of polyphagy (e.g., *Oxyopes salticus* and *Peucetia viridans* lynx spiders in cotton (Nyffeller et al. 1992)). (C) Since there are numerous other taxa of generalist predatory arthropods in a crop field, are spiders part of a larger guild set? This would depend on whether the focus is on ''community'' or ''assemblage'' guilds, *sensu* Jaksić (1981). Spiders as a group clearly represent the latter case, and given our arachnocentric focus and the potential importance of spiders in pest management, use of this term may be well-justified.

These questions are the essence of the guild conundrum for arachnologists, and the potential for circular reasoning is high. We justify our approach as follows. First, the primary focus of research on arthropods in agriculture *is* pest management. Since agroecosystems are

Table 1.—Existing spider guild classifications.

Spider family	Guild classification of spider taxa and the number of recognized guilds: Uetz 1977 (2 guilds)	Post & Riechert 1977 (11 guilds)
Pholcidae	Web-builders	—
Theridiidae	Web-builders	Scattered-line weavers
Dictynidae	Web-builders	Hackled band weavers
Linyphiidae	Web-builders/Wandering	Sheet line weavers
Micryphantidae	Web-builders/Wandering	Sheet line weavers
Hahniidae	Web-builders/Wandering	Hahniid spiders
Amaurobiidae	Web-builders	—
Filistatidiae	Web-builders	—
Agelenidae	Web-builders	Funnel web spiders
Araneidae	Web-builders	Orb weavers
Tetragnathidae	Web-builders	Orb weavers
Uloboridae	Web-builders	—
Anyphaenidae	Wandering spiders	Nocturnal running spiders
Clubionidae	Wandering spiders	Nocturnal running spiders
Gnaphosidae	Wandering spiders	Nocturnal running spiders
Lycosidae	Wandering spiders	Diurnal running spiders
Dysderidae	Wandering spiders	—
Pisauridae	Wandering spiders	—
Oxyopidae	Wandering spiders	Diurnal running spiders
Salticidae	Wandering spiders	Jumping spiders
Philodromidae	Wandering spiders	—
Thomisidae	Wandering spiders	Crab spiders
Heteropodidae (Sparassidae)	Wandering spiders	—
Sparassidae	Wandering spiders	—

human-managed monocultures, the arthropod ''communities'' they support are somewhat artificial, i.e., they represent temporary assemblages of taxa drawn together as a consequence of a variety of factors without a long history of evolutionary interactions.

Second, spiders colonizing agricultural fields are mostly generalist predators of arthropods (including other spiders); and while they may have evolved their particular niche exploitation patterns under different ecological circumstances, they exploit the same class of resources. Since the potential prey of spiders in agroecosystems may vary with microhabitat, season, time of day, and foraging strategy, spiders may constitute more than one ''assemblage guild.'' Under this set of circumstances, guilds will strongly mirror taxonomic relationships.

Finally, several recent studies have shown that assemblages of generalist predators (especially spiders and carabid beetles) can impact pest populations and reduce crop damage (Riechert & Bishop 1990; Snyder & Wise pers. comm.). Thus, an understanding of how spider assemblages in agroecosystems are organized is essential to study and employ these predators as pest control agents.

We will attempt here to construct spider guilds that may be found in agricultural fields. It should be made clear that these are preliminary designations, as data are often anecdotal and limited to a few representative species in any given family. New information on foraging behavior and microhabitat utilization patterns may change the basic assumptions. We will base our analysis on spider families, despite our own concerns about generalizations, because at least some information is available for each of the families commonly found in agroecosystems.

METHODS

Guild classification.—Spider families used in the determination of guilds were those listed as occurring in U.S. field crops cited in the

Table 1.—Extended.

Guild classification of spider taxa and the number of recognized guilds		
Nyffeler 1982 (3 guilds)	Riechert & Lockley 1984 (8 guilds)	Young & Edwards 1990 (5 guilds)
—	Scattered Line Weavers	Web-Matrix
Space-web spiders	Scattered Line Weavers	Web-Matrix
Space-web spiders	Hackled-Band Weavers	Web-Sheet
Space-web spiders	Sheet Web Builders	Web-Sheet
Space-web spiders	—	
—	—	Web-Sheet
—	Sheet Web Builders	Web-Sheet
—	—	Web-Sheet
Space-web spiders	—	Web-Sheet
Orb Weavers	Orb Weavers	Web-Orb
Orb Weavers	Orb Weavers	Web-Orb
—	Orb Weavers	Web-Orb
—	Nocturnal Running	Wandering-Active
Hunting spiders	Nocturnal Running	Wandering-Active
—	Nocturnal Running	Wandering-Active
Hunting spiders	Diurnal Running	Wandering-Active
—	—	Wandering-Active
Hunting spiders	Diurnal Running	Wandering-Active
—	Diurnal Running	Wandering-Active
Hunting spiders	Jumping	Wandering-Active
—	Crab	Wandering-Active
Hunting spiders	Crab	Wandering-Ambush
—	Crab	Wandering-Ambush
—	Crab	Wandering-Ambush

review of Young & Edwards (1990). To our knowledge, their study constitutes the most comprehensive treatment of spider species composition in agroecosystems available. Designation of spider guilds was based on ecological characteristics known for the family, or for a key species representing each family (Gertsch & Riechert 1976; Post & Riechert 1977; Gertsch 1979; Young & Edwards 1990; Nyffeler & Benz 1987; Nyffeler et al. 1992; Uetz, Halaj & Cady pers. obs.). Ecological characteristics relating to foraging manner, web type, microhabitat use, site tenacity and diel activity (Table 2) were subjected to a hierarchical cluster analysis using the unweighted pair group method with arithmetic averages using the MEGA software package (Kumar et al. 1993). Output of the analysis was organized into a dendrogram, and subsequent guild designations were based on the relative similarity of spider family clusters.

Spider guilds in agroecosystems.—We analyzed the dataset compiled by Young & Edwards (1990) to compare species richness of spider guilds among major U.S. crops. We also gathered additional information from literature cited within and from other sources to obtain quantitative data on spider guild structure of major crops. Here, relative abundances of spider guilds were averaged across: (1) same-crop references, and (2) datasets derived from several sampling techniques employed in the same study (e.g., sweeping *vs.* pitfall trapping), respectively, to obtain a more meaningful estimate of spider assemblage structure for a particular crop.

Analyses.—The similarity in spider species richness among crops was evaluated with the Sørensen qualitative coefficient C_S (Southwood 1992). We used our proposed guild classification to compare spider assemblage structure among individual crops using the species richness and spider abundance data. Similarity in spider guild composition was calculated with the proportional similarity index *PS* (Price 1984; Smith 1996). The similarity

Table 2.—Criteria used to construct new spider guild classification. 0 and 1 designate the absence of presence of the ecological characteristic, respectively, unless stated otherwise. Web use: 0—none; 1—sit on web; 2—hunt off web. Plant use: 0—none; 1—on foliage; 2—between plants. Site tenacity: 0—sedentary; 1—frequent site change; 2—mobile.

Family	Web	Web use	Tube web	Sheet web	Sheet/ space web
Agelenidae	1	1	0	1	0
Amaurobiidae	1	1	0	1	0
Anyphaenidae	0	0	0	0	0
Araneidae	1	1	0	0	0
Clubionidae	0	0	0	0	0
Dictynidae	1	1	0	0	0
Dysderidae	0	0	0	0	0
Filistatidae	1	2	1	0	0
Gnaphosidae	0	0	0	0	0
Hahniidae	1	2	0	1	0
Linyphiidae	1	2	0	0	4
Lycosidae	0	0	0	0	0
Micryphantidae	1	2	0	0	0
Mimetidae	0	0	0	0	0
Oxyopidae	0	0	0	0	0
Philodromidae	0	0	0	0	0
Pholcidae	1	1	0	0	0
Pisauridae	0	0	0	0	0
Salticidae	0	0	0	0	0
Sparassidae	0	0	0	0	0
Tetragnathidae	1	1	0	0	0
Theridiidae	1	1	0	0	0
Thomisidae	0	0	0	0	0
Uloboridae	1	1	0	0	0

among crops was then expressed in a form of dendrogram, with clusters constructed using the unweighted average linkage method (Pielou 1984). Cluster analyses were performed with STATISTICA (StatSoft 1997).

RESULTS AND DISCUSSION

Proposed guild classification.—The hierarchical cluster analysis produced a dendrogram which we used to construct spider guilds (Fig. 1). The breakdown of successive clusters appears to be based primarily on web use, web type, and microhabitat (but not diel activity), resulting in 6–8 clusters of spider families that can be considered guilds. The families of spiders separate first into web-building and hunting groups, and are further subdivided into clusters with obvious foraging similarities. Within the hunting spiders, two or four guild designations are possible, as a running spider cluster is distinct from a stalking/ambushing cluster; but separate guilds for foliage runners, ground runners, stalkers and ambushers can be designated within each of these clusters respectively. Within the web-building spiders, four distinct clusters correspond to previously-designated guilds (Riechert & Lockley 1984; Young & Edwards 1990): sheet web builders, wandering sheet/tangle weavers, orb weavers and 3-D space web builders.

Patterns of spider species richness in major crops.—The surveyed crops fall into three basic categories in terms of their spider fauna richness as suggested by Young & Edwards (1990). Cotton, soybean, and alfalfa support the highest number of spider species, followed by sugarcane, corn and peanut. Sorghum, rice and guar are the most species-poor crops (Fig. 2A). Besides vast differences in species richness, spider faunas of individual crops were also distinctly dissimilar (Fig. 2A). With the exception of alfalfa and soybeans (59.4% of species in common), values of species similarity were less than 45.0% for most crops. Since the vast majority of spider fauna in agricultural systems originates in natural habi-

Table 2.—Extended.

Space web	Orb web	Ambush	Stalk	Pursue	Ground	Vegetation	Plant use	Site tenacity	Diurnal	Nocturnal
0	0	0	0	0	1	0	0	0	1	0
0	0	0	0	0	1	0	0	0	0	1
0	0	0	0	1	0	1	1	2	0	1
0	1	0	0	0	0	1	2	1	1	0
0	0	0	0	1	0	1	1	2	0	1
1	0	0	0	0	0	1	1	0	1	0
0	0	0	0	1	1	0	0	2	0	1
0	0	0	0	0	1	0	0	0	0	1
0	0	0	0	1	1	0	0	2	0	1
0	0	0	0	0	1	0	0	1	1	0
0	0	0	0	0	1	1	1	1	1	0
0	0	0	0	1	1	0	0	2	1	0
1	0	0	0	0	1	1	1	1	1	0
0	0	0	1	0	0	1	1	2	1	0
0	0	0	0	1	0	1	1	2	1	0
0	0	1	0	0	0	1	1	2	1	0
1	0	0	0	0	0	1	1	0	1	0
0	0	1	0	0	0	1	1	2	1	0
0	0	0	1	0	0	1	1	2	1	0
0	0	1	0	0	0	1	1	2	0	1
0	1	0	0	0	0	1	2	1	1	0
1	0	0	0	0	0	1	1	0	1	0
0	0	1	0	0	1	1	1	2	1	0
0	1	0	0	0	0	1	2	1	1	0

tats, this pattern may likely reflect regional differences in the composition of spider fauna of adjacent habitats (Yeargan & Dondale 1974; Luczak 1979).

Despite notable differences in the number of spider species found in different crops and pronounced dissimilarities in their spider faunas (Fig. 2A), a remarkable constancy in the proportion of spider species within individual guilds was uncovered across all crops (Fig. 2B). For example, on average 16.9% of all spider species across the surveyed agricultural communities were stalkers. This pattern was consistent among all crops as suggested by the relatively low value of the coefficient of variation (CV) of 18.6%. Similarly, species of ambushers, foliage runners, ground runners, and sheet-web wanderers constituted a ‘‘fixed’’ percentage of the crop spider fauna (Fig. 2B). To our knowledge, this is the first report of species richness constancy reported for spider guilds and suggests the classification scheme outlined here may provide a good working basis for testing the significance of this pattern across a wider range of crop communities. Despite documented cases of similar proportional constancy of species numbers in arthropod guilds in several communities, a clear explanation for this natural pattern is lacking (Heatwole & Levins 1972; Moran & Southwood 1982). Heatwole & Levins (1972) suggest that the uniformity of trophic structure may mirror the spectrum of available species colonizing the habitat. In the case of agricultural systems, this explanation would imply the presence of a proportional constancy of spider species in adjacent natural habitats, a phenomenon awaiting an explanation of its own. Species responses to particular features of the habitat, or complex community interactions, may also dictate the resulting assortment of species (Heatwole & Levins 1972; Moran & Southwood 1982).

Spider guild structure of major crops.—Spider guild structure (proportional abundance) varied among individual crops (Fig. 3).

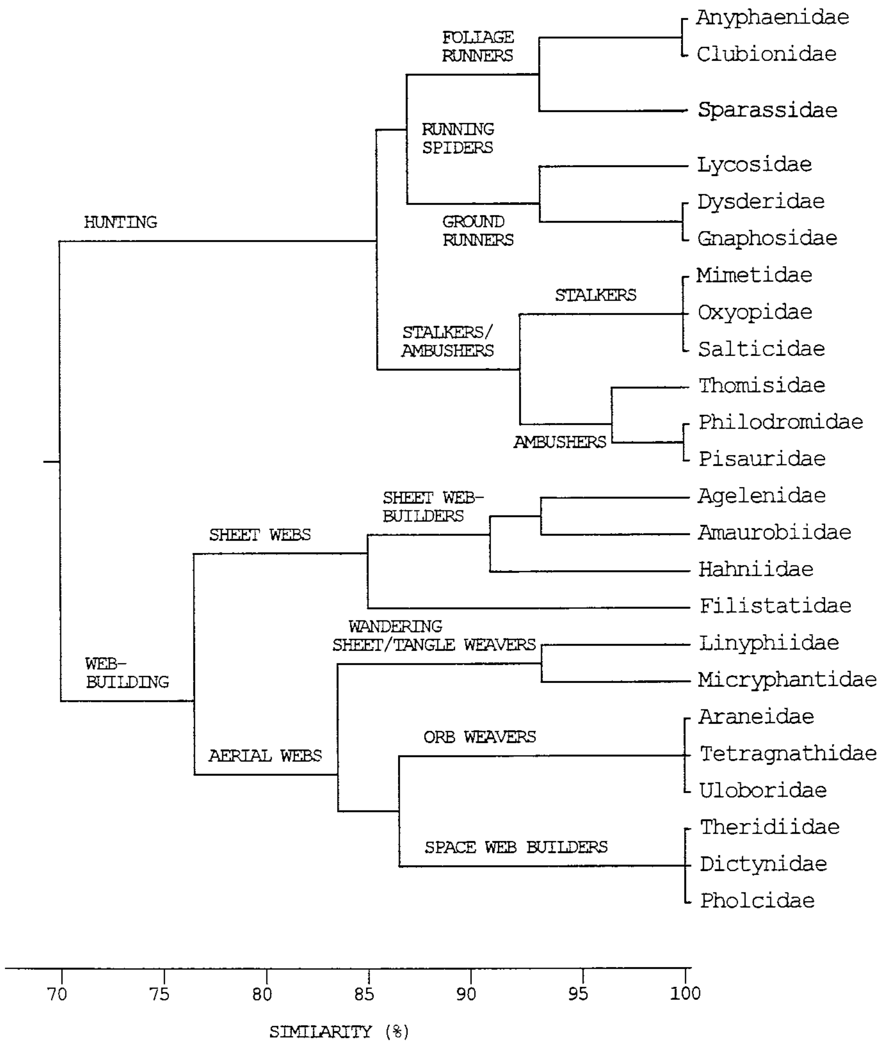

Figure 1.—Proposed spider guild classification dendrogram.

Based on structural similarity of spider guilds, two distinct groups of crops were separated: crops with spider fauna dominated by ground runners and web-wanderers (peanut, alfalfa, soybean, rice) and crops with a greater representation of orb weavers and stalkers (corn, cotton, sugar, sorghum). Similarly distinct assortments of spider guilds have been reported from a variety of crops (see reviews in Luczak 1979; Nyffeler 1982).

The most common explanation for observed patterns of spider guild structure are effects of the host-crop, including its structural diversity, microenvironment, or the level of disturbance (Luczak 1979; Young & Edwards 1990). Ample observations and more recent experimental evidence suggest that habitat structure maintains diverse spider assemblages (Uetz 1991; Wise 1993) and may be critical to successful insect suppression (Riechert & Lockley 1984; Riechert & Bishop 1990; Carter & Rypstra 1995; Marc & Canard 1997; and reviews in Wise 1993). Structural complexity may determine the guild composition of a crop's spider fauna and indirectly influence the level of herbivore damage (Young & Edwards 1990). Structurally complex crops providing a wider assortment of resources would be predicted to support a more diverse spider assemblage, thus increasing the chances of the

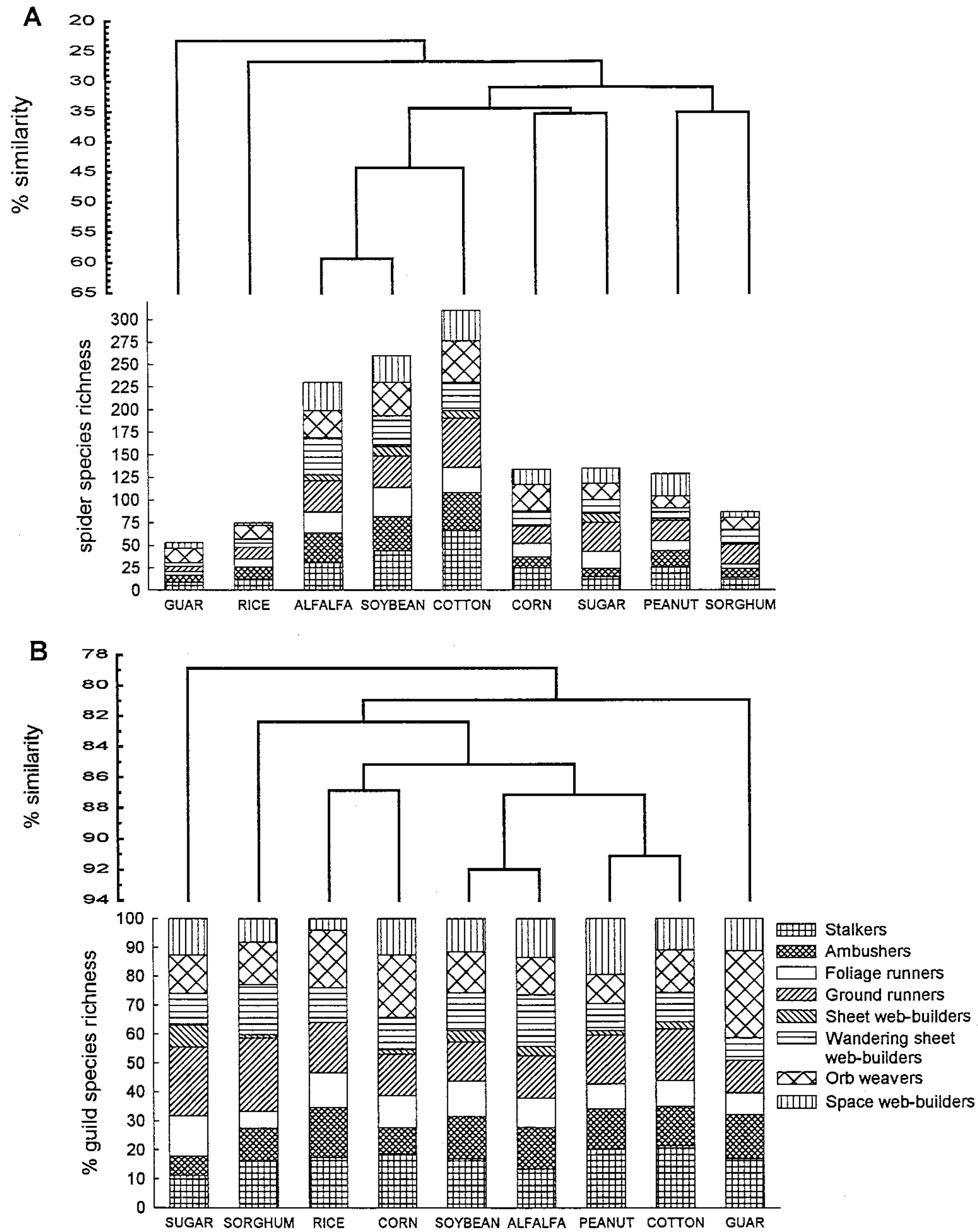

Figure 2.—A. Similarity in spider species composition among major crops. The dendrogram depicts clusters of the Sørensen qualitative coefficients. The bar graph represents the total number of spider species per guild. B. Proportional similarity (qualitative) in the relative species richness of spider guilds of major crops. The dendrogram represents clustering of values of the proportional similarity index. The bar graph shows the relative species richness of individual spider guilds. The figure is based on data in Young & Edwards (1990).

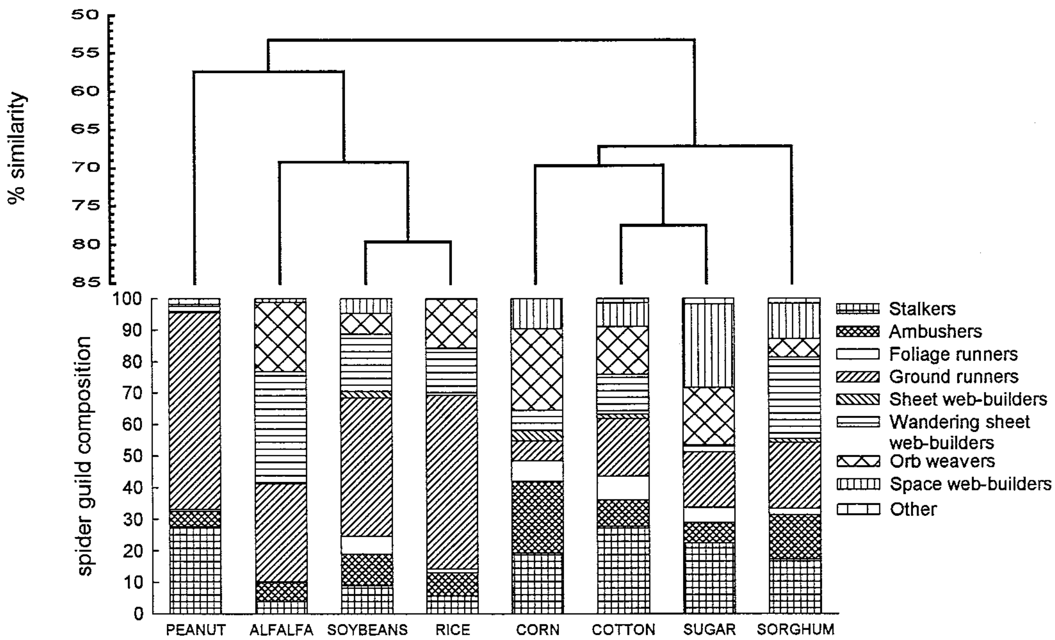

Figure 3.—Proportional similarity (quantitative) in the spider guild composition of selected crops. The dendrogram depicts clustering of values of the proportional similarity index. The bar graph represents the relative abundance of individuals spider guilds. The figure is based on data in Everly (1938); Whitcomb et al. (1963); Bailey & Chada (1968); Howel & Pienkowski (1971); Yeargan & Dondale (1974); Woods & Harrel (1976); LeSar & Unzicker (1978); Dean et al. (1982); Ferguson et al. (1984); Heiss & Meisch (1985); Agnew & Smith (1989); and Breene et al. (1993).

''best'' match between spiders and insect pests. On the other hand, structurally-simple crops may not develop an abundant and species-rich spider fauna, perhaps, lowering the importance of spider predation under these conditions.

Although it is reasonable to expect a significant influence of crop characteristics on structuring the resident spider community, the importance of adjacent habitats must also be considered (e.g., Webb et al. 1984; Duelli et al. 1990). Selective forces of the crop environment can act only on ''what is available,'' i.e., sets of species colonizing fields from neighboring habitats. For example, spider assemblages of alfalfa fields in Virginia are dominated by orb-weaving (42.7% of total spiders) and web-wandering guilds (37.6%) (Howell & Pienkowski 1971), while the same crop grown in California, and sampled with identical techniques (sweeping and D-vac sampling), is inhabited primarily by ground-running spiders (60%) and web-wanderers (33.6%), with orb-weavers constituting less than 2.0% of all individuals (Yeargan & Dondale 1974). Neighboring habitats may also influence the composition of crop spider fauna indirectly by modifying the dispersal of potential spider prey and predators in the patchy agricultural landscape (Alvarez et al. 1997; Polis et al. 1997).

Future directions.—Can the spider guild structure be predicted for a particular crop system? Although some patterns emerge from available studies, reliable predictions based on the current state of knowledge are not realistic. More data based on sound experimental design, studies combining several sampling techniques and detailed observations of spider habitat selection and diets, are critically needed to address this question. This forum provides a unique opportunity to address this critical issue and encourages more extensive work on spider guilds of major crops, similar to efforts of Luczak (1979), Nyffeler & Benz (1987), or Young & Edwards (1990). The following are our pleas to the arachnological and entomological audience: (A) Quantitative estimates of spider abundance. More attention should be given to recording and publishing quantitative information on spider guilds, as sole species composition data provide only partial answers to a multitude of questions regarding the structuring of spider guilds. (B) Observations of spider foraging and diet. Detailed observations of spider foraging and gathering of additional dietary data should be a critical component of a well-designed study. This information would help to confirm or reassess the validity of guild membership for individual spider species and further our limited knowledge of the significance of spiders as biocontrols. (C) The quality of adjacent habitats. Spider composition of the focal habitat is undoubtedly influenced by the quality of adjacent habitats via a multitude of direct or indirect channels. In order to understand the process of spider guild formation in the mosaic agricultural landscape, it is vital to record the context of crop fields as part of the sampling protocol, and if possible, to sample surrounding vegetation.

While arachnologists and others working in agroecosystems have been encouraged by results of recent studies suggesting that spiders can impact pest populations and reduce crop damage, most would agree that agricultural arachnology is still in its infancy compared with the breadth and depth of entomological research on integrated pest management and biological control. Baseline data on natural history and foraging behavior, necessary for any quantitative analyses of spider guilds within crop types, exist only for a limited number of species and are completely lacking for many spider taxa, including entire families. A better understanding of spider guilds, their composition and factors influencing spider community structure is therefore essential in future studies of the arthropod fauna of agroecosystems.

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