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ARCHITECTURAL FEATURES OF AGRICULTURAL HABITATS AND THEIR IMPACT ON THE SPIDER INHABITANTS

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ABSTRACT. The density and diversity of the spider community has been closely tied to the structural complexity of the local environment. For instance, soil dwelling spiders increase dramatically when the litter layer is enhanced because there are more retreats and hiding places and because temperature and humidity extremes are moderated. Web-building spiders are directly linked to the configuration of the vegetation because of specific web attachment requirements. Both correlative and experimental data support a tight relationship between spider density and habitat structure. Most of the available data show that agricultural practices which enhance the structural complexity of the environment (such as intercropping, mulching, and conservation tillage practices) enhance the density and diversity of the spider community. The key question regarding spiders in agroecosystems is, of course, whether they are in any way suppressing the activity of herbivores. Some studies uncovered a strong link between habitat complexity, spider abundance and plant productivity; but others have not, and the mechanisms by which spiders could exert a top-down effect are not clear. More investigation into the specifics of how habitat structure influences the predator-prey interactions in agroecosystems is needed in order to truly understand and manage agricultural production in a responsible manner.

Some of the earliest studies of spider habitat selection and community structure focused on the importance of architectural features of the environment. Clear relationships have been revealed between the physical complexity of the environment and spider abundance and diversity both across successional gradients (Lowrie 1948; Barnes 1953; Duffey 1978; Hurd & Fagan 1992) and across geographical regions (Greenstone 1984; Rypstra 1986). Surveys as well as manipulative studies have demonstrated that spiders respond to the diversity and complexity of the vegetation (Rypstra 1983, 1986; Robinson 1981; Greenstone 1984; Gunnarsson 1990; Halaj et al. 1998) and that cursorial spiders, in particular, respond to the depth and complexity of the litter layer (Uetz 1976, 1979; Bultman & Uetz 1982, 1984; Hurd & Fagan 1992). As pointed out by Uetz (1991), there are several reasons why spiders should be more sensitive to structure than other organisms. As a group, spiders perceive their environment using vibratory cues which are mediated through the substrate on which they live. Web spiders must anchor their prey capture device to the appropriate substratum and complex habitats provide appropriate sites for a greater range of sizes and types of webs. Finally, since all spiders are predators that can potentially consume one another, the extent to which they can coexist may strongly depend on their ability to move around and hide in a complex environment.

The literature on the responses of individual species of spiders and the community as a whole to habitat structure and complexity was comprehensively reviewed in the early 1990s (Uetz 1991; Wise 1993). The conclusions of both of these reviews suggest that, although clear associations exist, the specific aspects of the environment to which the spiders respond have not been adequately teased out. Diverse habitats provide a greater array of microclimate features, alternative food sources, and a greater number of possible retreat sites that can encourage colonization and the establishment of robust populations. More specifically, plant diversity and plant composition may influence predator diversity by changing foraging efficiency (Strong et al. 1984; Andow & Prokym 1990) and/or the nutritional quality of the herbivore prey (Price et al. 1980). Variations in the manner in which habitat structure affect interactions between predators and prey limit our ability to make broad generalizations regarding the specific mechanisms by which habitat diversity influences the spider community.

Numerous ecological models suggest that diverse producer communities will support more diversity at higher trophic levels. A recent study of Siemann (1998) demonstrates how complex testing this concept can be. He studied grassland communities with historical differences in fertilization into which he nested a more recent fertilization treatment. Past fertilization caused more than a four-fold decrease in plant species but resulted in no detectable differences in herbivore or detritivore species richness. Interestingly, arthropod predator (including spider) and parasite species richness was significantly higher in these plots. Siemann (1998) suggested that the predators might have become more abundant because they were more successful in foraging in the physically simpler environment but also mentioned that the shift in producer species composition may have changed the nutritional quality of the herbivores for the predator. This example runs counter to generalizations traditionally made by spider ecologists about the response of spider diversity to increased plant diversity (Uetz 1991; Wise 1993 and references therein). Siemann's results (1998) challenged our prior conceptions further in that his more recent fertilization treatments increased the diversity and abundance of all trophic levels in the grasslands. In this case, he explained the increase in herbivores and detritivores by suggesting that the increase in plant productivity allowed rarer species to persist. However, it is not at all clear why his two fertilizer treatments, which produced differences in the plant, herbivore and detritivore communities, had no apparent impact on predator diversity and/or abundance. Obviously the interactions in this trophic web cannot be explained by the basic principles we think we understand regarding how arthropod predators, including spiders, respond to habitat complexity. The only way to truly understand the responses of the predators in Siemann's (1998) experiments is to focus more directly on how the specific interactions between predators and their prey are mediated by the plant community.

Studies such as Siemann's (1998) may serve to make us more pessimistic regarding our ability to predict the potential impact of shifting agricultural practices on predatory arthropods. Since more than half of the predatory fauna in agroecosystems are spiders (Ferguson et al. 1984; Young & Edwards 1990), and it is known that changes in spider density can impact pest populations (Mansour et al. 1983; Riechert & Lockley 1984; Nyffeler & Benz 1987; Nyffeler et al. 1994), it would seem logical that the spider community would be a key component of integrated pest management strategies. Even though significant control of prey populations by assemblages of spiders has been suggested repeatedly (Clarke & Grant 1968; Riechert & Lockley 1984; Chiverton 1986; Agnew & Smith 1989), pest control strategies in North America rarely include them (Young & Edwards 1990). In order to increase the emphasis on spiders as agents of biological control, it is imperative to decipher exactly how shifting agricultural practices that change the habitat structure within relatively homogeneous fields influence the density, diversity and foraging behavior of spiders.

Although the agricultural literature was not specifically addressed in the reviews of Uetz (1991) and Wise (1993), a rich body of work has demonstrated that vegetation diversity of agroecosystems provides some measure of plant protection (Risch et al. 1983; Andow 1991a). Root (1973) proposed two hypotheses to explain the lower levels of herbivorous insects and pest damage in diverse systems. The resource concentration hypothesis suggests that specialist herbivores respond strongly to homogeneous systems of their host plant and cannot reach high levels in diverse systems. More critical to arachnologists is the enemies hypothesis which suggests that predators and parasites are more effective in diverse systems where alternative prey are present. Apparently the idea that biological diversity promotes community stability (the diversity-stability hypothesis of MacArthur 1955; Elton 1958) captured the attention of agriculturists studying the response of arthropods to diversity (Goodman 1975; Risch et al. 1983; Coll & Bottrell 1995). Thus, the notion that habitat diversification impedes the build up of pest populations became a paradigm even though empirical evidence in support of it is not any more rigorous than the identification of the specific features of a complex habitat to which the spider community responds.

Although the tendency over recent decades has been toward the simplification of the agricultural landscape, diversification within agricultural fields can easily be attained by intercropping, cover cropping, changing planting strategies and tolerating weedy culture. Overall, these practices tend to increase predator abundance (including spiders) and thus provide support for the enemies hypothesis (Ferguson et al. 1984; Coll & Bottrell 1995; Rypstra & Carter 1995; Balfour & Rypstra 1998; Costello & Daane 1998). However, it is not clear whether vegetation that provides abundant resources will act as a source or a sink for natural enemies in agroecosystems (Bugg et al. 1987; Kemp & Barrett 1989; Corbett & Plant 1993; Coll & Bottrell 1995; Costello & Daane 1998). For example, the greater availability of alternative food sources may reduce predation rate on a target pest (Ables et al. 1978). Non-host plants and high structural complexity may interfere with predator movement and alter the interactions between natural enemies and their prey (Perrin 1980; Andow & Prokym 1990). Alternative crops or weeds may actually draw predators away from the crop and thus reduce their impact on the herbivores (Bugg et al. 1987; Kemp & Barrett 1989; Rodenhouse et al. 1992). The specific manner in which diverse agricultural systems impact natural enemies in general or the spider community in particular needs to be quantified. Only then can we begin to make predictions about how the habitat changes that accompany diversification affect the role that spiders play in the food web.

There are a few examples of habitat manipulations in which the spiders appear to exert a top-down effect in the food web and increase plant production. In 1982, a USDA report mentioned that farmers in the Hunan region of China used straw bundles as retreats for spiders during irrigation of rice fields and that this minor habitat manipulation was associated with a 50-60% reduction in pesticide use. Kobayashi (1975) provided alternative prey in the form of fruit flies for spiders inhabiting rice paddies and observed an increase in spider populations and a decline in rice pests. However, the decrease in pest insects apparently came too late in the season to affect the amount of damage experienced by the plants.

Critical experiments regarding the importance of habitat manipulations to spiders were conducted in a mixed vegetable garden (Riechert 1990; Riechert & Bishop 1990). The habitat for the spiders was altered by adding mulch, which provides structure and moderates physical conditions for spiders. Prey density was altered by planting flowering plants that were meant to attract pollinators. These manipulations increased spiders densities, reduced pest insect densities, and led to reduced plant losses to herbivory. Further experimentation with spider removals and separation of the mulch and flower treatments demonstrated that the spiders that invaded the mulch were responsible for the observed increase in plant productivity (Riechert 1990; Riechert & Bishop 1990). Garden systems tend to be more diverse than standard agricultural fields and small scale manipulations such as the addition of mulch are relatively easy for motivated gardeners to implement if economic or production benefits were to be accrued. What is not clear from these experiments is the specific feature of the mulch (i.e., microhabitat moderation, structure, protection from predators, increased levels of prey, etc.) to which the spiders were responding.

Planting ground cover under emergent agricultural crops, such as vineyards and citrus groves, has been shown to increase spider abundance and diversity (Altieri & Schmidt 1985; Wyss et al. 1995; Costello & Daane 1998) but little effort has been invested in understanding how it affects pest control. Costello & Daane (1998) compared changes in the spider community in California grape vineyards with and without ground cover and attempted to relate it to the abundance and diversity of pest insects. Although there was no significant difference in the total spider abundance on vines with or without ground cover, *Trachelas pacificus* (Chamberlin & Ivie) 1932 (Araneae; Corinnidae), was significantly more abundant on vines planted with ground cover (Costello & Daane 1998). Even though Costello & Daane (1998) noted that *T. pacificus* is a major predator of the common leafhopper pests, they are pessimistic about the ability of ground cover to reduce pest populations by enhancing spider abundance. This question will not be resolved without a more mechanistic approach to understanding the specific interactions among the species that inhabit the different components of the habitat. For example, more detail regarding the effects of multiple predators and how they might take advantage of the movement of potential prey between the vines and the ground cover plants might explain effects that are not obvious from descriptive information about the distribution of organisms. Losey & Denno (1998a; 1998b) have described a situation where the escape response of an aphid upon encountering a predator foraging up on the vegetation made it more vulnerable to another predator on the soil surface. It is these kinds of complexities that must be incorporated more explicitly into our attempts to understand how spiders in complex habitats affect the food web.

Recently tilled and planted fields are barren habitats that are inhospitable for many arthropods, including spiders, yet this may be a critical time for establishing a community of predators capable of impacting plant production. In the spring, many spider species are actively engaged in widespread dispersal (Bishop & Riechert 1990), thus habitat manipulations that make the fields more attractive to them at this time may be particularly critical. Carter & Rypstra (1995) attempted to encourage spider establishment by placing crates in soybean fields just after planting. Their idea was that these crates would provide shade and some habitat structure while the plants were still small and then, as the plants grew, the spiders would move out into the vegetation where their impact on pest insects would be greater. Although their crates were colonized by spiders, the predominant species in the crates was a species that is not naturally abundant in soybean fields; and there was no evidence that these spiders moved out of the crates after the plants were mature. Nevertheless, across three seasons the biomass of insects consumed by the spiders in the boxes was negatively correlated with the amount of herbivory experienced by adjacent plants (Carter & Rypstra 1995). In two of three years, the herbivory experienced by plants in the vicinity of the boxes was significantly lower than in the fields at large or in areas where spiders were systematically removed. Although this manipulation was rather artificial and unlikely to be practical on a large agricultural scale, it demonstrates that small manipulations that enhance spider populations can have significant effects on herbivory in a conventional agroecosystem. However, it is again the case that no attempt was made to reveal the specific mechanisms by which the spiders interacted with the herbivores to cause the reduction in leaf damage observed.

Existing data provide strong evidence that simple habitat manipulations can affect spider populations and impact plant production in agroecosystems. Further experimentation must focus on how specific shifts in actual agricultural practices impact the spiders and, ultimately, the damage inflicted by herbivores. One example in which the aforementioned studies may be particularly applicable is the shift to conservation tillage (no-till) that has been occurring in North America over the last few decades (Sprague & Triplett 1986; Gebhardt et al. 1985; Ehrenfeld 1987). Fields managed under conservation tillage regimes experience lower levels of soil disturbance, which reduces erosion and allows the development of a much more complex litter layer (Gebhardt et al. 1985; Hendrix et al. 1986; Wardle 1995). Likewise, pressure to reduce the use of chemical herbicides may lead to increased invasion of weeds (Triplett & Lytle 1972; Wardle 1995; Pavuk et al. 1997). It is generally known that no-till fields support a more diverse resident arthropod community including pests and natural enemies (House & Stinner 1983; Stinner & House 1990; Tonhasca 1993). As mentioned above, spider communities respond to both soil litter (Bultman & Uetz 1982; 1984; Riechert & Bishop 1990) and plant diversity, including weed density, in no-till soybean systems (Rypstra & Carter 1995; Balfour & Rypstra 1998). Likewise, lower levels of insect damage have been observed in some no-till systems (House & Stinner 1983; Andow 1991b). Therefore, one would expect this to be a promising system, from both ecological and economic points of view, in which to study the impact of habitat changes on the spider community and how they may impact plant production.

Research needs to proceed toward developing a mechanistic understanding of how spiders and other natural enemies respond to specific habitat manipulations and how the habitat manipulations mediate predatory intensity. We need to uncouple the linkages between the structure itself and the specific features of the structure to which the spiders are responding so that we can quantify the ultimate effects on the food web. Although it is generally hypothesized that diversity enhances natural enemies by providing supplemental resources, few studies have actually documented this phenomenon experimentally. Given the variability of the community level responses observed, further investigations should incorporate a broad spectrum of specific effects such as the importance of spatial variation, changes in survivorship and fecundity, more detail on mobility and dispersal patterns, and the dynamics of the predator-prey interactions that occur within the agricultural systems (Corbett & Plant 1993). Only this level of comprehension will provide a basis for understanding the specific role of spiders in agroecosystems and ultimately enable us to predict the response of spiders to changes in agricultural practices.

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