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Mini-review

Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review

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Abstract

A review of the literature showed that spider abundance was increased by diversification in 63% of studies. A comparison of diversification modes showed that spider abundance in the crop was increased in 33% of studies by ‘aggregated diversification’ (e.g. intercropping and non-crop strips) and in 80% of studies by ‘interspersed diversification’ (e.g., undersowing, partial weediness, mulching and reduced tillage). It is suggested that spiders tend to remain in diversified patches and that extending the diversification throughout the whole crop (as in interspersed diversification) offers the best prospects for improving pest control. There is little evidence that spiders walk in significant numbers into fields from uncultivated field edges, but diversification at the landscape level serves to foster large multi-species regional populations of spiders which are valuable as a source of aerial immigrants into newly planted crops. There are very few manipulative field studies where the impact of spiders on pests has been measured in diversified crops compared with undiversified controls. It is encouraging, however, that in those few studies an increased spider density resulted in improved pest control. Future work needs are identified.

Introduction

Spiders, as generalist predators, differ from specialist predators in their mode of action against pests. While specialists are potentially effective at tracking a few pest species by functional, aggregative and reproductive responses, spiders can act against a broader range of prey types, even if prey populations are small. Special features of predatory behaviour, such as mortality of non-consumed pests in spider webs (Sunderland, 1999), and wasteful killing or partial consumption of prey by hunting spiders (Samu & Bíró, 1993), also contribute to the biocontrol potential of spiders. Prey preference, foraging methods and timing of predation vary between spider species, but seem to be complementary, and successful cases of pest suppression have been reported where spiders act as multi-species assemblages (Riechert, 1999). Numerous studies [e.g. see references cited in Greenstone (1999) and Reichert (1999)] support the contention that the effect of spiders on a prey population is related to the ratio (numerical or biomass) of spiders to prey. The precise effect of spider predation on a pest population will vary according to which other factors are influencing the rate of pest increase at the time. Web-making linyphiid spiders caused a peak mortality of 31 cereal aphids (*Sitobion avenae* (F.)) m^{-2} day^{-1} in a field of winter wheat (Sunderland et al., 1986), and it was estimated that, under the conditions prevailing at the time, predation by these spiders would have reduced peak aphid density by 37% (Fraser, 1982). De Barro (1992) showed that an 18 fold decrease (3.6 down to 0.2 per 195 cm^2) in the density of lycosid and linyphiid spiders inside enclosures in a perennial grass pasture caused a 16 fold increase in cereal aphid (*Rhopalosiphum padi* (L.)) density.

We suggest that the most promising option for utilising the specific predatory characteristics of spiders for the biological control of pests, is to increase their density within crops, as physically close to pests as possible. If this is achieved early in the cropping period, at the very start of the pest population increase phase, even a moderate spider density can create a favourable predator to pest ratio (Chiverton, 1986; Holland & Thomas, 1997). In such a situation spiders are likely to make a significant contribution to pest control even in cases where pests are not a preferred food (Toft, 1996). Rearing and release of spiders is not economically viable for the majority of crops and the enhanced density would, anyway, be transient without proper ecological underpinning. Agricultural diversification is, however, a potentially powerful means of achieving enhanced spider density in the right place at the right time.

We aim, by reviewing the literature, to test the hypothesis that diversification increases spider abundance and impact on pests. Heterogeneity at all scales is considered important for the preservation of spider diversity (Niemelä et al., 1996) and abundance (Samu et al., 1999). Within-crop diversification is reviewed because of its potential to increase spider density during the crop growing season, but we also review landscape diversification because of its significance for the longer term and larger scale maintenance of diverse and abundant populations of spiders.

It is well known that diversification of cropping systems can result in reduced pest populations (Risch et al., 1983; Andow, 1991; Altieri, 1994). It is also established that diversification might influence agroecosystems through various modes of action. Diversification can impede pests' host plant finding behaviour (Root, 1973; Wratten & van Emden, 1995; Finch & Kienegger, 1997; Finch & Collier, 2000), and it can affect crop yields directly (Theunissen & den Ouden, 1980; Tukahirwa & Coaker, 1982). Diversification might also impinge on pests indirectly, through boosting their natural enemies, such as spiders. Although spiders may interact with other natural enemies in affecting pest populations (Sunderland, 1999), this review focuses on spiders alone. There are very few studies where the role of diversifications in affecting pest populations, through the mediation of spider predation, has been investigated rigorously. We present those studies and explore how various aspects of diversification could increase the contribution of spiders to pest reduction.

Within-crop diversification

Techniques for increasing habitat diversity within crops include intercropping, weed strips, undersowing, mulches and weeds under the crop, and reduced tillage (which can result in the accumulation of straw mulch plus some weediness). The only example we found where within-crop diversification was associated with the actual decrease of a spider population was for the agelenid spider *Hololena nedra*, which was significantly less abundant on vines above ground cover than on vines above bare ground (Costello & Daane, 1998), even though this result was not consistent between years. In all other cases diversification either increased spider abundance (in 15 out of 24 (63%) studies – Table 1) or had no significant effect. Spider abundance was reported to be increased by reduced tillage in sorghum (Blumberg & Crossley, 1983) and sugar beet (Heimbach & Garbe, 1996), by weediness in soybean (Rypstra & Carter, 1995) and by straw mulches in cereals (Edwards & Lofty, 1979) and soybean (Wise et al., 1999). In addition to these examples, Table 1 summarises the results of studies for which differences in spider abundance in replicated diversified and control (undiversified) plots were compared statistically. Although diversification tends to increase spider abundance, there is considerable variation between case studies in the likelihood of this occurring. It would seem that some of this variability can be attributed to the spatial distribution of diversified habitat, and we explore this possibility in the next section.

Aggregated versus interspersed diversification

Intercropping and the inclusion of strips of non-crop plants (usually weeds) in the crop are examples of 'aggregated diversification', where there is a significant degree of spatial separation between crop types, or between weeds and crop. This contrasts with the other categories of diversification in Table 1 which are examples of 'interspersed diversification', where the diversification is below or amongst the target crop. Spider abundance in the crop was increased in 33% of cases by aggregated diversification compared with 80% for interspersed diversification. It is likely that this difference was, indeed, attributable to the nature

Table 1. Effects of within-crop diversifications on spider abundance (N.S. = no significant difference in spider abundance between diversified plots and control plots. Where the difference was significant the approximate degree of enhancement of spider abundance due to diversification is indicated)

Diversification method	Approximate enhancement factor	Main spider families	Crop	Country	Authors
Aggregated diversification					
Non-crop strips	N.S.	diverse (8 main families)	vegetables	USA	Riechert & Bishop, 1990
Non-crop strips	2	Araneidae	apple	Switzerland	Wyss et al., 1995; Wyss 1995,1996
Non-crop strips	N.S.	Salticidae, Oxyopidae, Thomisidae	apple	Hungary	Samu et al., 1997
Intercropping	3	Linyphiidae	squash - maize	USA	Letourneau, 1990
Intercropping	N.S.	Linyphiidae	carrot - lucerne	Sweden	Rämert, 1996
Intercropping	2	Linyphiidae, Araneidae, Salticidae	maize - bean	USA	Coll & Bottrell, 1995
Intercropping	N.S.	Tetragnathidae, Clubionidae	maize - bean	Canada	Coderre et al., 1989
Intercropping	N.S.	not given	maize - soybean	USA	Tonhasca & Stinner, 1991
Intercropping	N.S.	Lycosidae, Oxyopidae	cotton - lucerne	Australia	Mensah, 1999
Interspersed diversification					
Reduced tillage	N.S.	Linyphiidae, Lycosidae	spring cereals	Finland	Huusela-Veistola, 1998
Reduced tillage	N.S.[a]	not given	maize, soybean	USA	Tonhasca & Stinner, 1991
Reduced tillage	2	Linyphiidae	winter cereals	UK	Kendall et al., 1991
Reduced tillage	4	not given	sorghum	USA	House & Parmalee, 1985
Ground zone heterogeneity	13	Linyphiidae	maize	Belgium	Alderweireldt, 1994
Clover/grass mulch	N.S.	Linyphiidae	carrots	Sweden	Rämert, 1996
Straw mulch	10	diverse (8 main families)	vegetables	USA	Riechert & Bishop, 1990
Sawdust mulch	2	Lycosidae	asparagus	New Zealand	Wardle, 1995
Partial weediness	2	Tetragnathidae, Linyphiidae	soybean	USA	Balfour & Rypstra, 1998
Partial weediness	2	not given	maize	USA	Stinner et al., 1984
Partial weediness	3	Linyphiidae	winter wheat	UK	Topping & Sunderland, 1994c
Partial weediness	+ not given	Linyphiidae	winter wheat	UK	Feber et al., 1998
Partial weediness	3	Lycosidae, Linyphiidae	tomato	USA	Altieri et al., 1985
Undersowing	4	Lycosidae, Linyphiidae	tomato (clover)	USA	Altieri et al., 1985
Undersowing	2[b]	Corinnidae	grapes (barley, legumes)	USA	Costello & Daane, 1998

[a] Daytime search on foliage only.
[b] Varies with species.

of the diversification because the aggregated and interspersed subsets of Table 1 are otherwise fairly evenly balanced (e.g., both include annual and perennial crops, draw examples from Europe, North America and Australasia, and involve a mixture of spider families). There was also a tendency for the magnitude of the enhancement of spider abundance to be greater for interspersed than for aggregated diversification (Table 1). The largest enhancement factors were × 13 for increased ground zone heterogeneity (Alderweireldt, 1994) and × 10 for mulching with straw (Riechert & Bishop, 1990). We suggest that spiders tend to remain in diversified patches where conditions are optimal and that to increase spider density on and below crop plants, where they can impact maximally on pests, it is necessary to extend the diversification throughout the entire crop, as in interspersed diversification.

One of the convincing diversification experiments was performed by Alderweireldt (1994), who increased the heterogeneity of the ground in Belgian maize fields by spreading out clods of earth and by creating 10 cm deep circular holes of various diameters. The clods of earth did not result in a significant increase in spider density but the holes were colonised by web-building Linyphiidae, with *Bathyphantes gracilis* preferring 5 cm diameter holes and *Lepthyphantes tenuis* preferring holes with a diameter of 9.5 cm. In a similar manipulative experiment in wheat Samu et al. (1996) found that vacant holes were occupied by *L. tenuis* in a matter of days and territorial contests were observed between adult females attempting to occupy the same web in a hole. This suggests that scarcity of suitable web sites may be a factor limiting population size and that spider density might be augmented by the provision of more web sites. The results of the latter study may, however, have been due to a short-term redistribution of the existing spider populations into the 0.25 m^2 plots of holes and it remains to be determined whether provision of holes throughout a field would provide longer-term increases in spider density resulting from decreased emigration and increased reproduction.

Riechert & Bishop (1990) made quadrat counts of spiders in plots of mixed vegetables (spinach, radish, cabbage, sprouts, potatoes, tomatoes and maize), some of which had alternating rows of flowering buckwheat and vegetables (aggregated diversification) and others which were treated with a grass hay mulch (interspersed diversification). Flowering buckwheat had no consistent effect on spider density but the mulch increased spider density by 7–14 fold, depending on vegetable type. Spiders were the main predators present (accounting for 98% of predation events observed) and were taxonomically diverse but numerically dominated by diurnal running spiders (Lycosidae, Oxyopidae, Pisauridae) and sheet-scattered line weavers (Agelenidae, Hahniidae, Linyphiidae, Theridiidae). The authors suggested that spiders may have aggregated in the buckwheat strips in response to high prey densities and failed to move out onto the vegetables.

The resistance of spiders to move from the preferred segregated habitat to the less preferred one was demonstrated in several further studies. Mensah (1999) showed that spiders preferred lucerne to cotton and failed to move out onto cotton in cotton-lucerne intercrops. Jmhasly & Nentwig (1995) showed that, although weed strips in a field of winter wheat boosted the density of spiders (mainly Linyphiidae and Lycosidae) in the wheat, the effect declined at distances greater than 1.5 m from the strip.

Mechanisms whereby diversifications may affect spiders

In most studies reported in Table 1 the ecological mechanism underpinning successful augmentation was not rigorously demonstrated, but authors presented some evidence for involvement of various factors associated with microhabitat selection by spiders. The prime factors varied from species to species, and most frequently included i) the physical structure of the microhabitat, ii) microclimate, iii) the abundance of food, iv) disturbance, v) competition; vi) biotic interactions, such as attraction to silk, and vii) the avoidance of predation. Studies of the determinants of microhabitat selection and tenacity have been made mainly in non-agricultural habitats, but they provide a first indication of factors likely to also influence spiders in agricultural systems (Enders, 1977; Riechert & Gillespie, 1986; Uetz, 1991; Wise, 1993; Samu et al., 1999). Since microhabitat requirements vary between species, and the optimal microhabitat for an individual spider may also be temporally variable according to its changing needs, it follows that provision of a range of different microhabitats within a small area (= within-habitat diversification) will result in a greater range of spider species and a higher total density of spiders occupying the habitat. Individual spiders are more likely to remain in the habitat if it satisfies all their microhabitat requirements. Agricultural practices aiming at diversification will create various combinations of microhabitat-level factors that potentially affect local spider populations.

Reduced tillage results in, more weeds, more plant residues (therefore rich structure) and also less disturbance, higher soil surface moisture (Wardle, 1995) and a proliferation of detritivores (Robertson et al., 1994). Similarly, addition of mulches or manures to the soil surface of crops provides a more complex and diverse physical milieu, which gives spiders some protection from natural enemies, and improves microclimate, as well. Another structural enhancement, partial weediness (also termed ‘weedy culture’) allows selected weeds or non-crop plants to grow intermingled with crops (Andow, 1991). There are a number of measures that can be investigated to try and ensure that weeds are sufficient to encourage predators but do not reduce crop yield (Altieri, 1994). Weed cover improves the microclimate and increases the amount of alternative food in the form of herbivores and detritivores (Altieri & Whitcomb, 1979; Purvis & Curry, 1984). Weediness and undersowing increase the availability of structural support for webs, but there is also, as we have seen, potential for augmenting the density of ground zone web spiders by increasing the structural heterogeneity of the soil surface (Thornhill, 1983; Alderweireldt, 1994; Samu et al.,1996). Rich structure and the close spatial packing of different microhabitats could also support higher spider densities by reducing mortality, since there are various strands of evidence that have led authors to consider the risk of predation to be high when spiders move between microhabitats (Edgar, 1969; Enders, 1975, 1976, 1977; Vollrath, 1985; Bradley, 1993; Gunnarsson, 1996).

Mulching also increases the food supply for spiders, in the form of detritivores such as Acari, Collembola and Diptera (Edwards & Lofty, 1979; Larink, 1997). Similarly, undersowing crops with grass or clover increases the density of non-pest Hemiptera, Diptera and Collembola that are food for spiders (Vickerman, 1978; Grosse Wichtrup et al., 1985). There is evidence that spider density can actually be augmented by increasing the density of their fungivore and detritivore prey; this phenomenon was studied in a forest floor system (Chen & Wise, 1999), and may also apply to crop systems. Reduced tillage and the use of mulches and manures is equivalent to the addition of a food chain (the detrital food chain) that is virtually absent from conventional agriculture. Generalist predators are in a unique position in that they can, potentially, i) undergo rapid population development by feeding on detritivores enhanced by organic additives, and ii) also feed on herbivores, including pests, which belong to a different food chain (the grazing food chain). Although the addition of organic materials to crops dates back to the earliest days of agriculture (Gliessman et al., 1981; Pryor, 1998), the scientific investigation of its role in pest control is very much in its infancy.

Mechanisms of spider action in diversified habitats

Reduced pest populations and crop damage levels are sometimes associated with crop diversifications that increase spider abundance. Correlations of this sort do not prove a causal relationship, especially since there is a large body of evidence that diversifications can interfere with the normal host plant finding behaviour of the pest (e.g., the resource concentration hypothesis; Root, 1973; Cromartie, 1981) resulting in reduced pest populations. Manipulative experiments are necessary to prove the involvement of spiders in reducing pest density, and these are rare in the literature. A notable exception is the study of Riechert & Bishop (1990) who reported that pest numbers and damage in mixed vegetable plots were reduced when grass mulch was added. Spider densities were greater in mulched plots and the authors hypothesised that spiders were providing better pest control in the mulched plots. They proved that this was true by laboriously removing spiders by hand from some of the mulched plots, which then were found to have pest and damage levels similar to unmulched plots.

The mechanisms whereby diversification can affect pest populations via generalist predators such as spiders are, potentially, quite complex and may involve community interactions. Habitat diversification usually results in increases in the abundance and diversity of food for spiders and this, on the one hand, will promote rapid population growth leading to elevated spider densities, but, on the other hand, may result in spiders reducing their *per capita* feeding rates on pests in cases where pests are less favoured foods (e.g. for cereal aphids; Toft, 1995a; Sunderland et al., 1996). It has been hypothesised (Dempster & Coaker, 1974; Russell, 1989) that the closer the diversification is to the pest on the crop plant, the less distance the predator has to travel, and the more impact it will have on pest populations.

Various habitat diversifications (Table 1) might influence within-habitat movement and through this the pest control potential of spiders. Interspersed diversifications bring the enhanced spider populations into close proximity with crop plants, maximising the opportunity for switching between microhabitats. Some spiders will move vertically and search the crop plant. Even in apple orchards, some species found on the ground cover vegetation, below and between trees, were also found on the trees themselves (Samu et al., 1997; Yu-hua et al., 1997). Altieri & Schmidt (1986b), however, reported that high numbers of predators on cover crops did not always translate into higher numbers on the apple trees, and they advocated investigating whether mowing the cover crop would stimulate predators to ascend into the tree foliage. If the spider does not search the crop plant it may, nevertheless, encounter pests such as aphids and caterpillars that are voluntarily moving from one host plant to another, or that have been dislodged from the plant by wind, rain or as a response to escape imminent attack by natural enemies (Sunderland et al., 1997; Losey et al., 1999).

Spiders in close proximity to crop plants can also cause pest mortality by the ‘accidental’ action of their webs. Small pests, such as thrips, midges and aphids, may die by being caught in the webs of large spiders, even when they are ignored by the spider (Nentwig, 1987), and first instar cereal aphids were unable to escape from the sheet webs of even small linyphiid spiders in the absence of the spider (Sunderland et al., 1986). Linyphiidae, Dictynidae, Theridiidae and Agelenidae do not renew their webs daily, and the total web-cover due to linyphiids can be over half the area of a field (Sunderland et al., 1986), so these families are especially likely to contribute to pest control just by the action of their webs.

Structural diversity in a habitat can maintain diverse spider assemblages (Wise, 1993). Within-crop diversifications, by increasing the range of microhabitats available, are likely to increase the species richness of spiders in the crop. Assemblages of spider species have the potential to control pests in some crops where single species would fail (Riechert, 1999), and this is partly due to them having complementary niches (Nyffeler & Sterling, 1994; Marc & Canard, 1997), thus reducing ‘enemy-free space’ for the pests. A negative aspect of increasing spider species richness is an increase in the probability that intraguild predation will reduce pest control (Fagan et al., 1998; Wise et al., 1999). The plethora of potential interactions between habitat diversification, spider density and diversity, and pest control, underlines the need for rigorous manipulative studies [of the sort carried out by Riechert & Bishop (1990)] to determine which interactions predominate in agricultural systems.

Landscape diversification

Intensively cultivated arable fields are not self-contained systems for invertebrate predators, because their life cycles are interrupted periodically by severe agricultural practices such as ploughing, spraying, burning, etc. In the previous section various options were discussed which could reduce the severity of human impact, and make individual fields more attractive and retaining for spiders. Indeed, some of the best practices, such as reduced tillage, might promote continuous population growth for several years in such fields. Nevertheless, a predominant property of agricultural systems is the periodical decimation of the arthropod fauna, and, as a consequence, agricultural species must repopulate fields (Nyffeler et al., 1994; Thomas & Jepson, 1997; Wissinger, 1997). Thus the key to the pest control potential of spiders lies not only in the quality of the fields, but also in the quality of the surrounding landscape. The central question for the landscape-level approach to agricultural diversity is to determine which features of the agricultural landscape will result in a greater abundance and diversity of spiders in individual fields. This lesson could be learnt from studying the distribution and the dynamics of agricultural spider populations at the landscape scale.

Distribution of spider species in agricultural landscapes

Studying the agricultural spider fauna in a landscape context first leads to the question how are species from a regional species pool distributed among the mosaic of different habitat types. Luczak (1979) found that a broad range of Polish agrocoenoses were dominated by few spider species, which she called ‘*agrobiont*’ species. Agrobiont species must have good powers of dispersal (Luczak, 1979; Riecken, 1998) and be better equipped (e.g. through special life history strategies) than other species to survive under agricultural conditions (Toft, 1989; Young & Edwards, 1990; Wissinger, 1997). Agricultural habitats and structurally similar natural habitats can both harbour agrobiont species. In a seven years’ survey of the Hungarian arachnofauna in cereals, Samu et al. (2000) found that over 75% of all specimens belonged to only five species. The identity of these agrobiont species showed no significant regional variation in Hungary. Comparing the cereal fauna to that in nearby natural or semi-natural grassy habitats, only the two most dominant species (*Pardosa agrestis, Oedothorax apicatus*, representing 58.8%) were strongly positively associated with cereals, and they were significantly less frequently found in the grassy habitats. In contrast, considering all 107 non-incidental cereal spider species ($\geq$ 5 individuals), 103 were found in the grassy habitats as well (Samu, unpubl.). Uetz et al. (1999) also suggested that a relationship exists between agricultural and other habitat types. They noted that alfalfa in Virginia was dominated by different spider guilds than alfalfa in California (even though the same sampling methods were used), and they considered that this might have resulted from spider dispersal from contrasting adjacent habitats. Many other examples indicate that in agricultural habitats there is a strong dominance of few agrobiont species, but a certain similarity of the spider assemblage to that in natural habitat types also exists (Alderweireldt, 1993; Kemp & Barrett, 1989; Topping & Lövei, 1997).

The effect of neighbouring landscape units on spider distribution

Agricultural landscapes can vary in terms of the composition of field types, the type and timing of management in the fields, and by the presence of natural or semi-natural habitat patches. To study how the spatial configuration of such landscape elements may influence within-field spider populations, a number of studies chose the approach of following spider migration or of mapping spider distribution across ecotones (i.e. the border between different habitat patches).

In ecotones the local assemblage consists of species that are specific to this linear habitat, plus a mixture of the two neighbouring faunas, which overlap there. This often results in higher species richness in ecotones (Luczak, 1995). Field margins and hedgerows, which can be viewed as ecotone habitats, are often used for the diversification of agricultural landscapes, and they often show the ecotone enrichment effect. Non-crop spider species also live in habitats at the edges of fields and so species diversity is greater there than in the centre of fields (Kromp & Steinberger, 1992; Alderweireldt, 1993). The number (species and individuals) of cursorial wolf spiders (Lycosidae) tends to be greater at the edge than in the middle of fields, with the reverse often being the case for Linyphiidae, (Sunderland, 1987; Klimes & Sechterova, 1989; Glück & Ingrisch, 1990; Maelfait & DeKeer, 1990; Nyffeler & Breene, 1992; Huusela-Veistola, 1998), a family that contains many aeronaut species. Spiders can overwinter at the edges of fields (Maelfait & De Keer, 1990) and there is some potential for improving these habitats for spiders by vegetational diversification to include grass tussocks (Bayram & Luff, 1993) and wild flowers (Harwood et al., 1994; Thomas & Marshall, 1999), and by reducing the intensity of management practices (Feber et al., 1995).

The clarification of how field edges and neighbouring habitats contribute to within-field spider assemblages is especially important. The impact of such an input will depend on how far immigrating species penetrate into the fields and also on field sizes. When the physical similarity of neighbouring habitat patches was low, as was the case between farmland and various managed forests, the penetration zone was found to be not greater than a few metres (Downie et al., 1996) or a few tens of meters (Bedford & Usher, 1994). On the other hand, long transects through a range of habitats showed cropland predators to be ‘soft-edged’ species with diffuse distributions (Duelli et al., 1990), with potential to penetrate from non-agricultural to agricultural habitats. Overall, there seems to be little evidence that within-crop spider density is boosted by spiders walking from an edge into the immediately adjacent field, except over a penetration distance of a few metres (Altieri & Schmidt, 1986a; Alderweireldt, 1989; Kemp & Barrett, 1989; Dennis & Fry, 1992; Kromp & Steinberger, 1992). When spiders were marked in grass and oat fields a maximum of 5% were shown to have moved up to 5 m out of the habitat where they were marked (Kajak & Lucasiewicz, 1994). Weed strips sown at the edge of alfalfa fields in the USA contained a high density of spiders, but they did not walk out into the crop. The authors suspected that the weed borders were so hospitable to spiders that they had no stimulus to disperse (Bugg et al., 1987).

Rather than walking into field crops from edge habitats, spiders that have overwintered in edges and other habitats may ‘balloon’ and so join the regional pool of aeronauts in the spring (Greenstone et al., 1987; Sunderland, 1991; Blandenier & Fürst, 1998). Once spiders become airborne their flight direction and duration are determined, as far as is known, entirely by meteorological conditions (Bishop, 1990; Thomas, 1996). The majority of aeronauts probably travel only short distances per flight (Halley et al., 1996). When the weather is appropriate, however, spiders can re-balloon within a short period of time if the habitat where they have landed is not deemed suitable (Tolbert, 1977; Riechert & Gillespie, 1986). Tolbert (1977) observed some individual *Argiope* spp. spiderlings to re-balloon up to six times in a few hours and Heidger & Nentwig (1989) made similar observations on a dictynid spider species in a German winter wheat field.

The effect of the larger scale structure of landscapes

If there are no suitable reservoir habitats in the vicinity, crops can receive immigrants that have travelled from a different area (Bishop & Riechert, 1990; Topping & Lövei, 1997), but it is expected that crops close to reservoirs would receive more immigrants (Uetz et al., 1999). Aeronautic dispersal, and especially dispersal by repeated re-ballooning, is likely to be extremely risky because of the possibility of landing in unsuitable, life-threatening habitats, and because of increased exposure to predators. We therefore predict that diversified landscapes should harbour larger regional populations of spiders than simple landscapes because of reduced mortality during dispersal, and also because more species will find conditions that are suitable in diversified landscapes.

This hypothesis is very difficult to test, but recent modelling studies have demonstrated its plausibility (Topping & Sunderland 1994ab; Halley et al., 1996; Thomas, 1996; Topping, 1997, 1999). Inclusion of areas of set-aside and grassland in model landscapes increased metapopulation persistence and population densities of spiders over the whole landscape. In some agricultural landscapes there may be nearly continuous cropping (e.g. in the tropics), or a complement of crop types that senesce out of phase. In such situations, where spiders have the opportunity to balloon directly from a senescing crop to a young crop (Whitcomb & Bell, 1964; Burel & Baudry, 1995), the spatio-temporal pattern of cropping could be adjusted to minimise dispersal risk and thus enhance the scale of immigration into young crops (Parajulee et al., 1997; Prasifka et al., 1999).

We consider that the significance of diversification at the landscape level lies in the maintenance of large multi-species regional metapopulations of spiders. Crop habitats are often destroyed annually, causing severe reductions in spider populations, and interspersed diversifications within the succeeding crops can only be effective for pest control if they receive a sufficient influx of spider immigrants at an early stage of crop growth. The role of landscape diversification is to provide reservoirs, that are strategically placed spatially and temporally, and which act as safe havens for spider emigrants, and are then a source of immigrants into the crop fields.

Future work

This review has identified a need for the following studies, which we consider to be important for understanding the distribution and abundance of spiders in agroecosystems and for developing their potential as biocontrol agents.

Investigation of factors affecting microhabitat selection and tenacity by spiders in agroecosystems

Manipulative studies in natural habitats have determined how various spider species rank the importance of microhabitat features such as prey abundance, microclimate, level of disturbance and likelihood of encountering enemies, and the physical structure of the vegetation and ground. Such studies are now needed in agricultural systems. A knowledge of the physical and biotic conditions that would retain spiders in fields and maximise their reproduction would guide the development of practical and effective diversification techniques. Current techniques, such as reduced tillage, affect most of the microhabitat features listed above, and a more precise knowledge of which aspects are most important to spiders would enable the techniques to be refined and spider density to be enhanced.

Manipulative experiments to determine the impact of spiders on pests in relation to the degree of within-crop diversification

Although there is ample evidence that within-crop diversification often increases spider density, there is no certainty (given the complexity of ecological systems) that such increases will translate into improved pest control. Quantitative data are needed to describe how pest numbers (and consequent crop damage) respond to spider predation under different types of aggregated and interspersed diversification compared to undiversified control areas. Since diversifications can affect pests and crop yields directly, the role of spiders needs to clarified by manipulative studies. Where a diversification produces an increase in spider density and a reduction of pest density the spider population should be experimentally reduced in some plots to check whether pest density increases. This will not determine whether spiders alone are causing the pest reduction (because the spiders may be acting in concert with other natural enemies) but it will at least show whether spiders have a central role in the interaction.

Investigation of the role of reservoir habitats and the scale and timing of spider dispersal in the landscape

The current paradigm is that field edges and various categories of uncultivated ground act as important overwintering refuges for spiders. However, the quantitative data to support this contention are virtually absent. There is very little information about the density of agrobiont spiders in non-crop habitats during winter. It is possible that some types of overwintering habitat are much better than others and studies are needed to quantify this before the landscape can be managed to maximise the diversity and abundance of regional populations of spiders. Similarly, to be able to adjust the spatio-temporal pattern of cropping to capitalise fully on inter-crop dispersal of spiders we need to know when, and how far, spiders move. Ballooning is the most important mode of dispersal at the landscape scale and, although long-distance migrations are possible (Crawford & Edwards, 1986; Bishop & Riechert, 1990; Crawford et al., 1995; Toft, 1995b), the majority of individuals probably disperse by repeated short-duration flights. Behavioural studies are needed to determine the conditions (internal and external to the spider) that trigger ballooning (Weyman, 1993), and, just as importantly, what factors terminate ballooning motivation. This information would support more realistic estimates of mean dispersal distances which might then be tested with techniques such as the use of molecular markers (A'Hara et al., 1998). Data on the density of agrobiont spiders in reservoir habitats, and mean dispersal distances, would improve the precision of spatial dynamics models (e.g. Halley et al., 1996; Topping, 1999) in investigating the effects of landscape diversification on the abundance and distribution of agricultural spiders.

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