Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders

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Summary

1. The distribution and abundance of animals are influenced by factors at both local and wider landscape scales. Natural enemies of pests in arable fields often immigrate from the surrounding landscape, and are also influenced by local management practices. Thus, landscape diversification and farming methods may both enhance farmland biodiversity, but their relative roles and possible interactions have been little explored.

2. The relationships of ground-dwelling spiders (Araneae) to landscape features and to organic agriculture were studied in 12 pairs of organic vs. conventional fields of winter wheat *Triticum aestivum* along a gradient of landscape complexity.

3. High percentages of non-crop habitats in the landscape increased local species richness of spiders from 12 to 20 species, irrespective of local management. This indicates that larger species pools are sustained in complex landscapes, where there is higher availability of refuge and overwintering habitats.

4. Organic agriculture did not increase the number of spider species, but enhanced spider density by 62%. Additionally, spider density was positively related to the percentage of non-crop habitats in the surrounding landscape, but only in conventional fields.

5. Synthesis and applications. The species richness of ground-dwelling spiders in crop fields was linked to large-scale landscape complexity, while spider densities responded to local management practices. Organic agriculture benefits farmland spiders and augments the numbers of predatory spiders, thereby contributing to pest control. However, measures to conserve species richness must also take landscape-scale factors into account. Complex landscapes including perennial non-crop habitats should be preserved or restored to achieve high levels of spider diversity.

Key-words: Araneae, biodiversity, farm management, landscape complexity, organic farming, spatial ecology, winter wheat

Introduction

Animal communities depend on both local conditions and features of the surrounding landscape (Ricklefs 1987). The role of the wider landscape in structuring animal communities may be particularly important in highly dynamic habitats such as annual crops (Kareiva & Wenegneg 1995; Weibull & Östman 2003; Schmidt, Thies & Tscharntke 2004; Tscharntke & Brandl 2004). A major threat to farmland biodiversity is the expansion of intensive arable crops in many European landscapes during the past decades, leaving structurally simplified landscapes with little non-crop habitat (Stoate et al. 2001; Benton, Vickery & Wilson 2003). One consequence may be reduced diversity and abundance of invertebrate predators, which may in turn reduce the natural control of important crop pests (Riechert & Lawrence 1997; Schmidt et al. 2003). Never the less, landscape effects on local invertebrate species richness in farmland have remained relatively unexplored (Krebs et al. 1999). Recent exceptions are the positive effects of landscape complexity on the species richness of butterflies and ground beetles (Weibull & Östman 2003), and on trap-nesting bees and wasps (Steffan-Dewenter 2002).
Complex landscapes with high percentages of non-crop habitat can be expected to support more species than simple, crop-dominated landscapes. The movement of species between different habitats during their life cycle can lead to higher species richness in complex landscapes (Zobel 1997; Srivastava 1999). In agricultural landscapes, refuge habitats are of major importance for many arthropod populations during times when crops are disturbed (Landis, Watten & Gurr 2000; Sunderland & Samu 2000). Most spider species that are typically found in crops during summer emigrate from treated fields and overwinter predominantly in non-crop habitats (Marc, Canard & Ysnel 1999; Thomas & Jepson 1999; Thorbek & Bilde 2004; Schmidt & Tscharntke 2005a). Models have demonstrated how spider abundance can be enhanced by the availability of non-crop habitats at a landscape scale after events such as pesticide applications (Topping & Sunderland 1994; Halley, Thomas & Jepson 1996; Topping 1999). Hence, overall diversity and/or abundance may benefit from the availability of non-crop habitats in the landscape.

Organic farming aims to promote beneficial invertebrates by prohibiting the use of synthetic pesticides and mineral fertilizers. The positive influence on arable weeds is well documented (Menalled, Gross & Hammond 2001; Hyvonen & Salonen 2002), and densities of bats and dung beetles are higher on organic farms compared with conventional agriculture (Hutton & Giller 2003; Wickramasinghe et al. 2003). Effects of organic farming on predacious arthropods are less clear (Glück & Ingrisch 1990; Booj & Noorlander 1992; Moreby et al. 1994; Feber et al. 1998; Pfiffner & Luka 2003; Weibull & Östman 2003; Hole et al. 2005). Pfiffner & Niggli (1996) pitfall-trapped 108%, 97% and 161% more spider individuals in organic than in conventional fields during 3 years. They found similar patterns in ground beetle (Coleoptera: Carabidae) and rove beetle numbers (Coleoptera: Staphylinidae), but did not test for differences in species richness. In addition, there is little information on whether landscape effects on arthropods differ between conventional and organic management (Östman, Ekborn & Bengtsson 2001). Landscape effects may be stronger in conventional fields because arthropod populations depend more on immigration, or in organic fields because they can accommodate more immigrants. We tested the relative influence of landscape effects and agricultural management on spiders in winter wheat *Triticum aestivum* L. fields using a paired-field approach along a gradient of landscape complexity. In particular, we examined which properties of the spider community are determined at local and landscape scales.

**Materials and methods**

**STUDY SITES**

In the study region around the city of Göttingen, Germany, 12 non-overlapping landscape sectors of 1·5-km radius were chosen along a gradient from structurally simple, with >80% arable land, to structurally complex, with >50% non-crop habitats. Simple and complex landscapes were interspersed. In each landscape sector, one conventionally and one organically managed winter wheat field (according to EC Regulation 2092/91) was chosen, thus avoiding differences in landscape context between the two management styles. The pairs of organic and conventional fields were selected to be as similar as possible in all respects other than management. Diversity and percentage cover of all weeds were recorded three times during the growing season on four plots of 3 × 10 m per field. Field size was not significantly different between conventional and organic fields (3.9 ± 0.6 ha vs. 3.1 ± 0.4 ha, t = 1.3, P = 0.21). All studied fields were bordered by grassy margins that were mowed once per year. The majority of adjacent crops for both field types were conventional winter cereals. In organic fields, winter wheat was grown after a mixture of clover and grass, while the preceding crops of conventional winter wheat were mostly winter wheat and oilseed rape. Organic fields were fertilized with manure and weeds were controlled mechanically, while conventional farms applied mineral fertilizers, herbicides, fungicides and usually one insecticide spray in June. For details on conventional farming practices in the study region see Roschewitz, Thies & Tscharntke (2005).

**SPIDER SAMPLING**

Spiders were sampled using four pitfall traps per field, arranged in a 10 × 10 m square, two traps 15 and 25 m from the field edge, respectively. The traps consisted of 0.5 L plastic cups with an upper diameter of 8.8 cm. Three centimetres beneath the top edge, pieces of wire mesh with 1·9 cm wide quadratic openings were inserted to prevent vertebrates from entering. Each trap was filled with 0·12 L of a mixture (1:2) of ethylene glycol (antifreeze) and water plus a few drops of detergent, and was protected from rain with 25 × 25 cm acrylic glass roofs. The traps were operated twice for 14 days, starting on 8 May and 28 June 2002. This follows the sampling scheme suggested by Duelli, Obrist & Schmatz (1999) for collecting the maximal proportion of a full season catch with minimal effort. Catches were transferred to 80% ethanol. Pitfall trap catches reflect a combination of each species’ abundance and likelihood of being trapped (largely determined by walking activity). We assumed that numbers of individuals captured per field reflected between-field differences in absolute densities for each species (Topping & Sunderland 1992). Juvenile spiders are underrepresented in pitfall traps, so our results and conclusions hold predominantly for adult populations. Adult spiders were identified to species, and juveniles to family, the nomenclature following Platnick (2004). Females of *Oedothorax apicatus* and *Oedothorax retusus* were not distinguished. Species richness was calculated using only adult individuals.
The percentage of all non-crop habitats within a radius of 1·5 km around the study fields was calculated as a measure of landscape complexity, based on official digital thematic maps (ATKIS, Digitales Landschaftsmodell 25/1; Landesvermessung und Geobasisinformation, Hannover, Germany, 1991–96). The percentages of other land-use types and their diversity were calculated for the same landscape sectors. Arable land covered on average 59%, and non-crop habitats comprised mainly forest (21%, predominantly deciduous), grassland (13%, mainly hay meadows) and urban (6%, including gardens).

Redundancy analysis (RDA) was performed on square-root-transformed spider densities to visualize similarities and differences of the assemblages occurring in the different fields. Correlations of environmental variables with the composition of the assemblage were tested using Monte Carlo permutations (MCP; ter Braak & Smilauer 2002). Effects of (i) conventional vs. organic management and (ii) the percentage of non-crop habitats in the surrounding landscape on species richness and density were analysed with general linear models (GLM; SAS proc mixed; SAS institute, Cary, NC), using the two sampling periods as repeated measures and the landscapes (1–12) as random blocking factors. Non-significant interactions were backwards eliminated, and the residuals checked for normal distribution. At the family and species levels, Spearman’s rank correlations and Wilcoxon’s signed rank tests were used, because the assumptions for parametric tests were not always fulfilled. Increased probabilities of falsely rejecting null hypotheses in multiple comparisons were avoided by using Bonferroni corrections, and by calculating the overall probability of the observed frequency of outcomes falling below the nominal significance level \( \alpha = 0·05 \) with Bernoulli equations (Moran 2003). Results were considered significant when at least one of these two criteria was met. Arithmetic means ± standard errors are given in text and figures.

Results

SPIDER ASSEMBLAGES

Eight thousand and thirteen spider individuals from 69 species were sampled, 7911 of which were adult (see the Appendix). Spider assemblages of organic and conventional fields were separated on the first axis of the RDA (Fig. 1). Local management practices explained this difference (MCP, \( F = 2·4, P = 0·01 \)), together with the directly related factors wheat stem density (higher in conventional fields), weed cover and weed species richness (both higher in organic fields). The second axis represented the landscape gradient. The percentage of non-crop habitats in the surrounding landscape was correlated with this community gradient, although only with marginal significance (MCP, \( F = 1·7, P = 0·09 \)). Spider assemblages in the organic and conventional fields of each landscape had similar scores on the second axis. Neither field size, diversity of land-use types, percentage of forest or percentage of grassland in the surrounding landscape showed significant correlations with the spider assemblages (MCP, \( P > 0·1 \)).

Spider densities were 62% higher in organic than conventional fields (Fig. 2 and Table 1). Additionally, densities during May were positively correlated with the percentage of surrounding non-crop habitats in conventional but not organic fields (conventional \( y = 85 + 1·86x, r = 0·70, \alpha = 0·012, \) organic \( y = 228 + 0·47x, r = 0·09, \alpha = 0·78 \)). To examine the positive effect of organic farming on spider densities more closely, the three genera captured in the highest numbers were tested separately (Table 2). Densities of the money spider Oedothorax spp. and wolf spider Pardosa spp. were 88% and 103% higher in organic than in conventional fields, respectively. In contrast, densities of the commonly ballooning money spider Erigone spp. and the cumulated densities of all other genera were not significantly influenced by management.

Species richness rose with high percentages of non-crop habitats in May (Fig. 3a; bivariate: \( y = 10·4 + 0·14x, r = 0·63, \alpha = 0·001 \); overall GLM: Table 1) but not in July (Fig. 3b; \( r = 0·19, \) NS). Management did not influence species richness, nor did it interact with the effect of landscape complexity (Fig. 3 and Table 1). The positive effects on spiders
influence of non-crop habitats on species richness during May was not attributable to a particular (sub) family (Table 3). While the correlation coefficients were positive for Erigoninae, Linyphiinae and Lycosidae, none of the correlations were significant. The pooled richness of the remaining families also showed a non-significant but positive correlation with the percentage of non-crop habitats.

Table 2. Effects of organic farming on the densities of the three most numerous captured spider genera. t-tests for matched pairs on average numbers per field pooled over both sampling dates

<table>
<thead>
<tr>
<th>Spider Genera</th>
<th>Conventional</th>
<th>Organic</th>
<th>d.f.</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Erigone spp.</td>
<td>55 ± 6</td>
<td>67 ± 13</td>
<td>11</td>
<td>−0·9</td>
<td>0·40</td>
</tr>
<tr>
<td>Oedothorax spp.</td>
<td>101 ± 25</td>
<td>191 ± 42</td>
<td>11</td>
<td>−3·3</td>
<td>0·007</td>
</tr>
<tr>
<td>Pardosa spp.</td>
<td>49 ± 14</td>
<td>100 ± 14</td>
<td>11</td>
<td>−4·7</td>
<td>0·001</td>
</tr>
<tr>
<td>Other genera</td>
<td>47 ± 6</td>
<td>50 ± 8</td>
<td>11</td>
<td>−0·6</td>
<td>0·55</td>
</tr>
</tbody>
</table>

**SPIDER SPECIES**

In spite of the clear patterns at the assemblage level, there were few significant effects of landscape or management at the species level and over all 69 species there was no significant relationship between density and management (sign test: \( Z = 0·38, P = 0·7 \)). Abundances between conventional and organic fields were compared using Wilcoxon’s signed rank tests for the 27 species with six or more occurrences, and four species showed significant
effects on spiders

Landscape vs. management

Discussion

The effects of landscape context and local management on spiders in cereal fields were differentiated in this study. The landscape context influenced species richness irrespective of management type, while organic and conventional fields differed in the composition of the spider assemblage and in their overall density. The higher spider densities under organic management suggest more favourable habitat conditions. As spider habitats, organic fields may be superior to conventional fields in three respects. First, omitting pesticides may either directly reduce spider mortality or increase food availability through a reduction in the mortality of spider prey. In the present study, no insecticides had been applied prior to the first spider sampling, but spider densities were already higher in organic than in conventional fields at that time. Therefore, insecticides alone could not have caused the observed difference. Secondly, spiders may benefit from higher weed populations in organic fields, which provide higher structural complexity and hideouts at the soil surface, and potentially increase the availability of herbivore prey. Cover of arable weeds was higher in the organic fields compared with the simplest landscapes compared with the simplest landscapes, approximating an 80% higher density in the most complex landscapes than the ground-dwelling species in the current study (Halley, Thomas & Jepson 1996; Thomas, Brain & Jepson 2003; Schmidt & Tscharntke 2005b). Additional to the landscape effect on species richness, spider density in conventional fields during May was positively related to the percentage of non-crop habitats in the surrounding landscape. However, both conventional and organic fields were mostly bordered by conventionally managed land, and only 17% of the arable land in the study region was organic (Niedersächsisches Landesamt für Statistik, personal communication). Therefore, further-reaching benefits could be expected if organic farming became more widespread and spanned more continuous tracts of the agricultural landscape.

Species richness in wheat fields rose with the proportion of non-crop habitats in the surrounding landscape, with no apparent difference between organic and conventional management. Thus, spider communities in wheat fields were not at maximum levels (Srivastava 1999; Loreau 2000) and fewer species arrived in wheat fields in crop-dominated landscapes. This suggests that fewer species exist in structurally simple landscapes (Landis, Watten & Gurr 2000; Sunderland & Samu 2000). Alternatively, fields could have been too isolated from source habitats to be reached by certain species, but this seems unlikely as the distances from the traps to the next grassy field margin (small-scale heterogeneity) were equal in all study sites. As is typical for pitfall traps (Topping & Sunderland 1992), our catches were dominated by wolf spiders (Lycosidae) and money spiders (Erigoninae). With the exception of Erigone atra and Erigone dentipalpis, commonly ballooning species were poorly represented (Weyman, Sunderland & Jepson 2002). Other important species in crops (the majority of Linyphiidae, Araneidae and Theridiidae) disperse more aerially and may respond differently to the landscape context than the ground-dwelling species in the current study (Halley, Thomas & Jepson 1996; Thomas, Brain & Jepson 2003; Schmidt & Tscharntke 2005b). Additional to the landscape effect on species richness, spider density in conventional fields during May was positively related to the percentage of non-crop habitats, approximating an 80% higher density in the most complex landscapes compared with the simplest ones. This suggests that density in conventional fields was determined by landscape-wide immigration processes, while organic fields developed more self-sustained populations.

CONCLUSIONS

Organic farming enhanced the density of ground-dwelling spiders in wheat fields, while high percentages of non-crop habitats mainly increased species richness, particularly in late spring. Spiders are important predators in arable crops and the control of herbivores depends on high predator densities (Landis, Wratten & Gurr 2000; Symondson, Sunderland & Greenstone 2002; Schmidt et al. 2003). Hence, enhancement of spider numbers through organic farming may improve natural pest control and contribute to agricultural productivity (Östman, Ekborn & Bengtsson 2003). Landscape complexity in this study enhanced spider diversity irrespective of management, and increased density in conventional fields. High percentages of non-crop habitats in the landscape may thereby alleviate the harmful effects of intensive agriculture on spider communities. As parasitoid wasps (Hymenoptera parasitica), ladybirds (Coleoptera: Coccinellidae) and ground beetles (Coleoptera: Carabidae) also benefit from landscape diversification, it is clear that complex landscapes host more biological control agents overall (Elliott, Kieckhefer & Beck 2002; Schmidt, Thies & Tscharknkte 2004; Portauf et al. 2005; Thies, Roschewitz & Tscharknkte 2005). In addition to local measures, such as organic farming, that may increase numbers of natural enemies, complex landscapes with a high proportion of perennial non-crop habitat should be preserved and developed to achieve high levels of biodiversity in the farmed countryside.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals_suppmat/JPE/JPE1014/JPE1014sm.htm.

Appendix. Species list with average spider densities in conventional and organic fields

References


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