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Abundance and diversity of spiders (Araneae) in barley and young leys

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Abstract. The fauna of surface-active spiders was studied in 12 cereal fields, with two types of subcrop, and in four young (17 months old) perennial leys (grass/clover). The fields were located in the southeastern (A), central (B) and western (C) parts of Norway. In total, 3945 spiders were caught from May to September 2004, using pitfall traps. Linyphidae was the most numerous family, with *Erigone atra* Blackwall 1833 representing 56% of all trapped individuals. The total numbers of spider species and individuals were significantly higher in leys than in barley at sites where both crops were present (sites A and B), with on average 11 species and 93 specimens in barley, and 20 species and 393 specimens in leys. Thus, young perennial leys appeared to provide a better habitat for spiders than did cereal fields, as has previously been documented for older perennial leys. The use of multi-species crops instead of a single crop species undersown in cereals, tended to result in higher spider species diversity, but it did not influence the total number of specimens. An ordination (DCA) showed a clustering of the spider fauna from the same site, but no clear separation between main crop types (ley vs. barley) was apparent. The main crops, subcrops, and the surrounding environs of the cropped field seem to affect the diversity and abundance of spiders.

Keywords: Cereal, community structure, farming, meadow

High abundance and diversity of spiders is considered to be important in both conventional and organic cropping systems because of the predatory function of spiders (Nyffeler & Benz 1987; Alderweireldt 1994; Marc et al. 1999; Kuusk et al. 2008). In organic farming, one has to rely on natural enemies, such as spiders and predatory insects, for pest suppression because the use of insecticides is not permitted. All spiders are true predators and constitute a heterogeneous group in terms of their feeding strategies, size, activity patterns, and dispersal modes (Marc et al. 1999). The diversity of many predatory insects and spiders is under pressure in agricultural landscapes (Kålås et al. 2010). With regard to pest suppression and the maintenance of biodiversity, both the density and diversity of spider populations are of interest in agricultural fields. The spider fauna in agricultural areas has so far been little studied in Norway (Andersen 1990; Pommeresche 2002, 2004).

Field borders and perennial crops, such as leys and pastures, often host more species and a higher number of spiders than do annual crops and cereal fields (e.g., Huusela-Veistola 1998; Ratschker & Roth 2000; Pommeresche 2004; Schmidt & Tscharntke 2005; Batáry et al. 2012). This may be related to a greater structural heterogeneity of perennial crops and a lower frequency of destructive soil tillage operations. There is a positive relationship between the spider fauna and the complexity of the local habitat (Rypstra et al. 1999; Gravesen 2008). Sunderland and Samu (2000) concluded that structural heterogeneity within the crop was more favorable for spider density in the cropped field than was structural heterogeneity in adjacent habitats. They found that spiders tended to settle in non-cropped and/or intercropped strips rather than within the main crop, unless the latter was diverse in structure.

Grasses are commonly undersown in cereals in order to suppress weeds and as a catch crop to prevent leaching of nutrients after the annual crop has been harvested (Sturite et al. 2007). Legumes are often used as subcrops in organic systems in order to improve the nitrogen supply (e.g., Reynolds et al. 1994). Perennial leys are usually established by undersowing in barley in order to obtain a cash crop in the year of establishment. One might expect that increasing habitat heterogeneity, by using multi-species instead of single species subcrops in cereals, would result in increased spider density and diversity. However, to our knowledge this assumption is as yet untested.

Soil tillage and harvesting operations cause disturbance and thereby reduce spider populations (Thorbek & Bilde 2004; Öberg & Ekbom 2006). For instance, 26 d after tillage, 93% fewer spiders were found in plowed fields and 80% fewer in non-inversive, deeply loosened fields than in untilled fields (Thorbek & Bilde 2004). Many lycosids appeared to survive the soil cultivation at sowing (harrowing and drilling) of cereals, but few linyphiids did (Öberg & Ekbom 2006). All the same, the linyphiids re-established themselves, or even increased in number, within a few weeks of such cultivation. Many linyphiids found in cultivated fields are pioneer species with a high potential for aerial dispersal, but some [e.g., *Oedothorax apicatus* (Blackwall 1850)] may also disperse cursorially; i.e., by walking (Thomas & Jepson 1999; Lemke & Poehling 2002). The length of time since crop establishment is thus a factor to consider when evaluating spider communities in agricultural systems.

Spiders respond to diversification at both local and landscape levels. A heterogeneous landscape, including perennial crops and field borders, is an important stimulant to the immigration of spiders into newly established crops (Sunderland & Samu 2000; Öberg et al. 2007, 2008; Schmidt-Entling & Döbeli 2009). At a landscape level, perennial grassland and field borders increase the density of aerially dispersing linyphiids, whereas adjacent field margins have the most influence on the density of cursorial lycosids (Huusela-Veistola 1998; Öberg et al. 2008; Schmidt-Entling & Döbeli

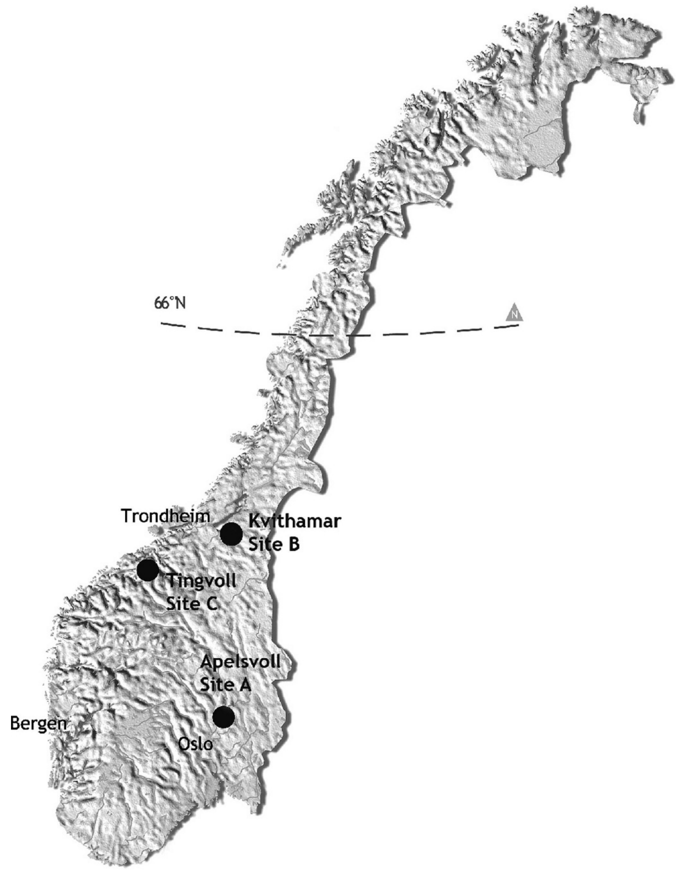

Figure 1.—Map of Norway showing the three sites (black dots) where samples were collected. The broken line shows the Arctic Circle.

2009). Also, the species diversity in both families is influenced by the heterogeneity of both the landscape and the adjacent habitat (Bishop & Riechert 1990; Öberg et al. 2008; Schmidt-Entling & Döbeli 2009).

The present study explores the spider fauna in young perennial leys and spring barley fields with mono-species or multi-species subcrops. Our aim is to describe the community structure and diversity of spiders found among these young but structurally differing crops, one to two seasons after abrupt and radical disturbances caused by soil tillage.

METHODS

From May to September 2004 we sampled surface-active spiders from 12 fields with spring barley and four fields with first-year leys located in southeastern (site A), central (site B), and western (site C) Norway (Fig. 1, Table 1). The barley was subcropped with either a mixture of grasses and clovers or ryegrass alone, or else grown without any subcrop. The barley and all subcrops were sown in April/May 2004. The first-year leys were undersown in spring barley the previous spring (2003) and consisted of 80–90% (w/w) perennial grasses and 10–20% clover species. These leys were 17 months old at the end of the spider sampling period. Annual mean (1961–1990) precipitation and temperature were 600 mm and 3.6 °C at site A, 890 mm and 5.3 °C at site B, and 1160 mm and 5.6 °C at site C.

Site description.—*Site A:* The Apelsvoll cropping system experiment (Eltun 1994; Korsaeth 2008) comprised two replicates of six different four-year crop rotations/systems laid out in a randomized block design. Each system consisted of

Table 1.—Characteristics of fields at three sites (A, B and C) in Norway, where spiders were sampled from May to September 2004. Sampled crop (corresponding to "Field") is marked with bold letters. The main crop is mentioned first and the subcrop after the slash. All leys were mixtures of grasses and clovers.

Field	Cropping system	Sampled crops (in bold) within crop rotation	Tillage	Plant protection
A1a, A1b	Conventional arable	**Barley-** Potatoes- Wheat – Oats	Autumn plowing	Chemical
A2a, A2b	Conventional arable	**Barley/ryegrass**- Potatoes -Wheat/ryegrass - Oats/Italian ryegrass	Spring harrowing	Chemical
A3a, A3b	Organic arable	**Barley/ley-**1st yr. ley -Wheat/ryegrass – Oats + peas	Spring plowing	Harrowing
A4a, A4b	Organic dairy	Barley/ley **- 1st yr. ley** - 2nd yr. ley - 3rd yr. ley	Spring plowing	Harrowing
B1a, B1b, B3a, B3b	Organic dairy	**Barley/ley (B1) - 1st yr. ley (B3)** -2nd yr. ley – Oats+peas	Spring plowing	Harrowing
C1a, C1b	Organic dairy	**Barley/ryegrass** - 1st yr. ley - 2nd yr. ley.- 3rd yr. ley	Spring plowing	Harrowing
C2a, C1b	Organic dairy	**Barley/ley** - 1st yr. ley- 2nd yr. ley- 3rd yr. ley	Spring plowing	Harrowing

four 15 m × 30 m rotation units (fields). We sampled spiders from fields with spring barley (A1–A3) and ley (A4) (Table 1). The barley was managed either conventionally without subcrops (A1), conventionally with perennial ryegrass as a subcrop (A2), or organically, with a grass-clover mixture (ley) as a subcrop (A3). Just before sowing the barley (13 May 2004), mineral fertilizers were applied to crops A1 and A2. Pesticides (herbicides, fungicides and insecticide) were used in the two latter systems. Crop A3 did not receive any chemical plant protection or fertilizer. The barley was harvested on 5 September 2004. The ley was not fertilized, and it was harvested on 14 June and 18 August 2004. The surrounding habitats of the cropping system experiment constituted mainly other crops (potatoes and cereals), field borders and some woodland and gardens.

Site B: The Kvithamar cropping system (Bakken et al. 2006; Johansen et al. 2008) comprised two replicates (blocks) of a four-year crop rotation/system. Each of eight rotation units was 55 m × 25 m. We sampled spiders from two replicates of two crop types, one with undersown spring barley (B1) and the other with ley (B3) (Table 1). Cattle slurry was spread before sowing of the barley on 4 May 2004 in B1, and on 22 April 2004 in B3. The barley was harvested on 24 August and the leys on 15 June and 1 September the same year. The system was located in an agricultural landscape predominantly consisting of cereal fields and some perennial leys, with permanent field borders and small roads.

Site C: This organically managed dairy farm was cropped with spring barley in a 3–5 year rotation with perennial grass-clover leys. In addition, there were permanent pastures nearby. We sampled spiders in two replicated transects within fields of spring barley, subcropped with either annual ryegrass (C1) or a grass-clover mixture (C2) (Table 1). Cattle slurry was applied prior to sowing the barley (15 May 2004). Field C1 was about 300 m × 100 m and C2 was 80 m × 25 m. The surrounding habitats included perennial leys, field borders, trees, drystone walls, and roads.

Sampling and identification.—We measured the activity of surface-dwelling spider species by sampling spiders in pitfall traps. These consisted of plastic jars, 6.5 cm in diameter, filled one-third with 50% (vol.) propylene glycol. Some droplets of a liquid detergent were added to break the surface tension. Spiders were sampled in eight rotation types with two replicates of each (a and b). Five traps were placed 2 m apart in a row at the center of each of the 12 sampled fields at sites A and B. At site C, we placed two replicate sets of traps more than 25 m apart, one in the center (b) and one (a) a bit closer to the field border in the two fields.

Pitfall trapping is the most commonly used sampling method for spiders (Hänggi et al. 1995), although it samples mostly surface-active individuals (Tretzel 1955; Topping & Sunderland 1992; Southwood & Henderson 2000). Since ground-dwelling species are more numerous in cultivated fields than the web-building/foliage-dwelling species (Nyffeler & Benz 1987), pitfall traps seemed most practical for our purpose. We were aware that this created a bias in both the diversity and the density, and thus we refer to the data as surface-active specimens.

During the sampling periods in 2004 (25 May–2 Sept at site A, 19 May–2 Sept at site B and 26 May–4 Sept at site C), we emptied the traps three to four times. They were removed from the fields during management operations involving machinery, and put back shortly afterwards. We pooled the five traps within fields and over time. Hence, each of the 16 fields was represented by one sample. Only adult spiders were identified and counted. The identification keys of Roberts (1993a,b, 1995) and Almquist (2005) were used, and nomenclature and taxonomy were in accordance with Platnick (2012).

Statistics and data analysis.—We analyzed the number of sampled individuals per trap day found in each field using ANOVA for each site separately. Field type (four levels at site A, two levels at site B, and two levels at site C) was regarded as a fixed factor and replicate (block) as a random factor. We conducted multiple comparisons of (least-square) means according to a Tukey's test. The data for sites A and B together (n = 12), were also subjected to ANOVA, with crop (ley, barley) as the fixed factor and site (A, B) as the random factor. The procedure MIXED in the statistical package SAS (SAS Institute Inc. 1999) was used for all analyses. In all tests, significance was assumed at P-levels < 0.05. We applied the same models for square-root transformed data for the total number of species found in each field.

The total number of species was also analyzed in a GLMM, implemented using the lmer function in the lme4 package (Bates & Sarkar 2006) developed for R (R Development Core Team 2008). We included site and crop as nested random factors in the model and principal crop type (ley, barley) as the fixed factor. The fixed factor was tested by comparing models with likelihood ratio tests. Models were made sequentially and reduced by backward elimination of non-significant effects ($P < 0.05$) (Crawley 2007; Zuur 2009).

A Detrended Correspondence Analysis (DCA) was run with CANOCO for Windows 4.5 (ter Braak & Smilauer 2002). We made the analysis and ordination of both the spider communities and the eight most abundant species from a dataset that included the species and their abundance in each field, from the total trap period. Rare species were down-weighted. The ordination placed similar communities of spiders close together in the diagram, while those less similar in species composition and abundance were placed further from each other (Jongman et al. 1995).

RESULTS

We trapped and identified 3945 spiders to species at the three sites. Thirty-seven species belonged to the Linyphiidae, thirteen to the Lycosidae, and seven to other families (Table 2). The most numerous species in the dataset were agrobiont linyphiids, where *Erigone atra* Blackwall 1833 represented 56%, *Oedothorax* spp. 13%, *E. dentipalpis* (Wider 1834) 5% and *Bathyphantes gracilis* (Blackwall 1841) 5% of all the trapped individuals. Most of the individuals of the genus *Oedothorax* were *apicatus* (Blackwall 1850) and even fewer were *retusus* (Westering 1851). The most numerous lycosids were *Pardosa palustris* (Linnaeus 1758) 8% and *P. amentata* (Clerck 1757) 3%, representing 58% and 21% of the lycosids, respectively.

The number of spiders varied between sites and crops (Tables 2 and 3). The mean number of spiders was 93 (1.02 ind. trap-day^{-1}) in barley fields (n = 8) and 393 (4.22 ind. trap-day^{-1}) in ley fields (n = 4), averaged across sites A and B, where both crops were present. The corresponding numbers of

Table 2.—The species and number of spiders found in barley and ley fields, sampled with pitfall traps, from May to September 2004. Only species names of spiders with two or more individuals in the material are shown, whereas the totals (sum) include all data. The number of spiders from the two replicates (a and b) are shown as a sum. For details about the cropping systems and management, see Table 1.

	A1a/b	A2a/b	A3a/b	A4a/b	B1a/b	B3a/b	C1a/b	C2a/b	% tot.
Linyphidae									
Erigone atra Blackwall, 1833	16	22	43	217	121	436	605	739	56
Oedothorax spp. (*apicatus* > *retusus*)	42	50	162	168	30	71		1	13
Erigone dentipalpis (Wider, 1834)	1	1		18	6	15	64	108	5
Bathyphantes gracilis (Blackwall, 1841)	1		7	6	73	81	5	10	5
Meioneta rurestris (C. L. Koch, 1836)	8	20	11	24	5	13		1	2
Porrhomma spp.	1		2	1	18	9			1
Bathyphantes parvulus (Westring, 1851)					5	22	10	2	1
Savignia frontata Blackwall, 1833		2	2	13	1	13	2		1
Leptorhoptrum robustrum (Westring, 1851)			1		4	8			
Allomenga scopigera (Grube, 1859)	1		1				2	3	
Collinsia inerrans (O. P.-Cambridge, 1885)							4	4	
Diplostyla concolor (Wider, 1834)		4		1		1		1	
Meioneta affinis (Kulczyn'ski, 1898)				1		1	1	2	
Diplocephalus latifrons (O. P.-Cambridge, 1863)				2				2	
Gongylidiellum vivum (O. P.-Cambrigde, 1875)							1	2	
Silometopus elegans (O.P.-Cambridge, 1872)		1		1			1		
Centromerita bicolor (Blackwall, 1833)				3					
Dicymbium nigrum (Blackwall, 1834)				1		1			
Neriene clathrata (Sundevall, 1830)								2	
Bathyphantes nigrinus (Westring, 1851)								2	
Dicymbium tibiale (Blackwall, 1836)		1		1					
Erigonella hiemalis (Blackwall, 1841)				1				1	
Gongylidium rufipes (Linneaus, 1758)							1	1	
Erigone longipalpis (Sundevall, 1830)							1		
Sum Linyphidae	70	103	230	461	263	674	698	884	86
Lycosidae									
Pardosa palustris (Linnaeus, 1758)	8	6	9	234	8	38	4	2	8
Pardosa amentata (Clerck, 1757)	2	1	7	36	11	30	4	21	3
Pardosa fulvipes (Collett, 1876)	2		1	37					1
Pardosa pullata (Clerk, 1757)	1		2	7	2	14	1	2	1
Pardosa riparia (C. L. Koch, 1833)		1	1	11	1				
Trochosa ruricola (De Geer, 1778)	2		3	3					
Pardosa agrestis (Westring, 1861)					5	3			
Pardosa nigriceps (Thorell, 1856)					1	3			
Trochosa terricola Thorell, 1856							1	1	
Pardosa paludicola (Clerk, 1757)				2					
Sum Lycosidae	15	8	23	330	29	89	10	27	13
Other spider families									
Pachygnatha degeeri Sundevall, 1830				5		2	2	4	
Pachygnata clerki Sundevall, 1823				1	2	5			
Robertus neglectus (O. P.-Cambridge, 1871)			1	3	1				
Micaria nivosa L. Koch, 1866			2						
Sum individuals	85	111	256	801	295	770	711	916	
Numbef of trap days	85	85	85	84	105	105	94	94	

species were 11 and 20. When comparing all fields at sites A and B, those cropped with leys had significantly higher numbers of species (ANOVA, $F_{1,9} = 25.3$, $P < 0.001$), specimens (ANOVA, $F_{1,9} = 62.0$, $P < 0.001$), specimens of linyphiids (ANOVA, $F_{1,9} = 54.2$, $P < 0.001$) and specimens of lycosids (ANOVA, $F_{1,9} = 10.6$, $P = 0.010$), than had fields cropped with barley (Table 3). The analyses of total number of species performed by GLMM confirmed the significance of the differences between principal crop types (GLMM, $z = 3.3$, $P < 0.001$). The number of individuals in the barley fields at site C was high (4.9 ind. trap-day^{-1}), and comparable to the number trapped in first-year leys at the other sites (Table 3). Linyphidae was the most numerous family in all fields at all sites. The proportion of lycosids was higher overall in leys than in barley crops.

The most numerous species in the cereal fields at sites A and B were the ballooning linyphiids *E. atra* (both in A and B) and *Bathyphantes gracilis* (B) and the more cursorial *Oedothorax* spp. (A), whereas *E. atra* and *E. dentipalpis* dominated in the cereal fields at site C (Table 2). The most abundant species in the leys were *E. atra* and *Oedothorax* spp. Of the lycosids, *P. fulvipes* (Collett 1876) was found only at site A, in southeastern Norway, and mostly in leys. *Pardosa palustris* and *P. amentata* were found at all sites, with slightly higher numbers of individuals in the ley fields.

Table 3.—Number of individuals and spider species trapped in different crops at three sites (A, B and C). Means within sites marked with different letters were significantly different from each other ($P < 0.05$). The main crop is mentioned first and the subcrop after the slash. All leys were mixtures of grasses and clovers. See Table 1 for details on the management.

Crops within site	No. of individuals per trap-day			Total no. of species
	Lycosidae	Linyphiidae	Total	
A1, Barley	0.09	0.41a	0.50a	8.0a
A2, Barley/ ryegrass	0.05	0.61a	0.65a	9.5a
A3, Org. barley/ ley	0.14	1.35a	1.51a	12.5b
A4, 1st year org. ley	2.00	2.74b	4.77b	21.5c
Standard error (SE)	0.42	0.27	0.43	
B1, Org. barley/ ley	0.14	1.25	1.41a	14.0
B3, 1st year org. ley	0.42	3.21	3.67b	18.0
Standard error (SE)	0.18	0.17	0.18	
C1, Org. barley/ ryegrass	0.05a	3.71	3.78	14.0a
C2, Org. barley/ ley	0.14b	4.70	4.87	17.0b
Standard error (SE)	0.02	0.52	0.53	

At site A, the number of species was significantly higher in the organically managed barley undersown with a grass-clover mixture (A3) than in the conventionally managed barley with ryegrass subcrop (A2) (Tukey, $t_3 = -5.3$, $P = 0.038$) or in barley without any subcrop (A1) (Tukey, $t_3 = -8.3$, $P = 0.011$) (Table 3). At site C, a higher number of species (ANOVA, $F_{1,1} = 235.9$, $P = 0.041$) and more individuals of lycosids (ANOVA, $F_{1,1} = 285.8$, $P = 0.038$) were found in barley undersown with grass-clover ley (C2) than in barley undersown with ryegrass (C1) (Table 3).

The ordination (DCA) showed a gradient of fields (spider communities) along the first two DCA axes (Fig. 2). Communities from the same site appeared to cluster, with site A mostly having the lowest scores on both axes, site C having the highest scores, and site B being intermediate. No clear clustering appeared relating to crops or subcrops. The gradient along DCA axis 1 explained 42.2%, and the gradient along DCA axis 2 an additional 12.8% of the variation in the species data, giving a total of 55.0% explained variation. The ordination also showed where the species were most abundant (shown for the eight most abundant species, Fig. 2). The first axis appeared to be related to the presence of species that were predominantly site-specific. For example, *Oedothorax* spp. and *Meioneta rurestris* were found mainly at sites A and B (low score on DCA axis 1), whereas *Erigone dentipalis* was mainly found at site C (high score on DCA axis 1). The second axis appeared to be related to the variation in species abundance between fields. As an example, *P. palustris* had the highest score on axis 2 (Fig. 2) and also the highest coefficient of variation between fields (data not shown), whereas *Pardosa amentata*, *M. rurestis, and Oedothorax* spp. were more evenly distributed between fields (lower coefficients of variation) and scored lower on axis 2.

DISCUSSION

In this study, the most abundant species were the agrobiont linyphiids *E. atra*, *Oedothorax* spp., *E. dentipalpis,* and *B. gracilis*. These were also among the most abundant species in agroecosystems in several other European studies (Thorbek & Bilde 2004; Schmidt & Tscharntke 2005; Öberg et al. 2007). We found *O. apicatus* in both young perennial leys and in cereals. By contrast, Schmidt and Tscharntke (2005) reported that this species was more frequently found in cereal crops than in perennial grass fields, due to its cursorial dispersal and tolerance of sparsely vegetated soil. We found more *Pardosa amentata* and fewer *Tenuiphantes tenuis* (Blackwall 1852) than Schmidt & Tscharntke (2005) reported for German agroecosystems. In the German study, Schmidt & Tscharntke (2005) found significantly more *Pardosa palustris* and *Pardosa pullata* (Cleck 1757) in perennial systems than in annual crops and wheat.

Several studies have revealed higher numbers of specimens and/or species in perennial meadows and leys than in cereal fields (e.g., Schmidt & Tscharntke 2005; Batáry et al. 2012). After collecting 4700 spiders, Schmidt & Tscharntke (2005) recorded forty-seven species in annual crops ($n = 26$), mainly wheat fields, and eighty in perennial grassland ($n = 16$). This indicated much higher numbers of species than we found, due to a variety of factors, but clearly indicating a higher number of species in older perennial systems. Our study shows that this divergence was also clear in relatively young leys (17 months old). Moreover, our results demonstrate a positive effect of ley on the spider fauna even in small experimental fields, where one may assume that the surrounding environment plays a relatively large role.

The inclusion of undersown crops in the barley, which probably made the spatial structure more similar to that in the ley fields, appeared to be an insufficient means of creating a spider habitat comparable to that of ley. So what can explain the favorable effect of ley on spider abundance and diversity? We believe that one reason is the longer length of time that has passed since plowing (one season) in the case of ley. Plowing has been found to be more harmful to spiders than has grass cutting (Thorbek & Bilde 2004).

Another factor, which may favor ley as a spider habitat, irrespective of its age, may be its relatively rich invertebrate fauna on which spiders feed. Spider abundance and diversity are influenced by the prey fauna, both at ground level and within the vegetation, which is thus of great importance for spider competitiveness. Collembolans and dipterans are especially important for the recruitment of juvenile spiders (Toft 2005; Gravesen 2008) and, along with aphids, they are also an important food source for adult spiders (Nyffeler & Benz 1988; Alderweireldt 1994). Collembola density and

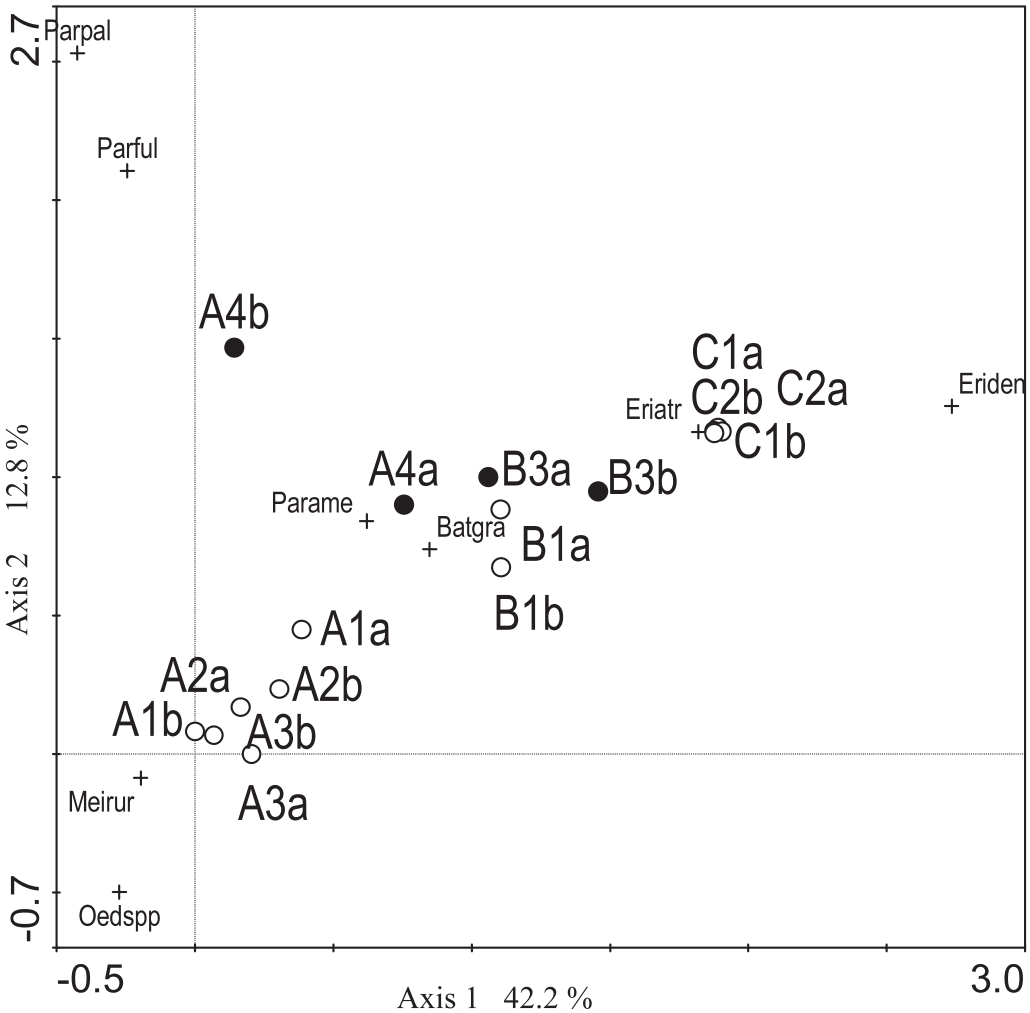

Figure 2.—Ordination (DCA) of the spider communities in different fields, based on species composition and density. Rare species were down-weighted. Black circles are spider communities from leys; open circles are spider communities found in spring barley. The ordinations of the eight most abundant species are shown with + and abbreviated name (Batgra = *Bathyphantes gracilis*, Eriatr = *Erigona atra*, Eriden = *Erigone dentipalpis*, Oedspp = *Oedothorax* spp., Meirur = *Meioneta rurestris*, Parame = *Pardosa amentata*, Parful = *Pardosa fulvipes*, Parpal = *Pardosa palustris*).

diversity have been found to increase with plant species richness in grassland (Sabals et al. 2011) and to respond positively to the use of liquid animal manure (Sokolowska & Seniczak 2005).

When looking solely at barley fields, the outcome at site C showed that a subcrop consisting of several species (ley mixture) resulted in a higher number of spider species than a single-species subcrop (ryegrass). This may be explained by the positive effects of increased spatial structure and prey fauna, as discussed above. The findings at site A were similar, as there were significantly more species in fields with multi-species subcrops (A3) than in fields with ryegrass as the only subcrop (A2). At site A, however, the difference may have been caused by a difference in pesticide use, rather than subcrop, since the management between A2 and A3 was very different. Several studies have shown that the use of pesticides decreases the density and/or diversity of spiders, but exceptions have also been found (e.g., Andersen 1990; Stark et al. 1995; Marc et al. 1999; Huusela-Veistola 1998). Chemical treatments influence the spider fauna either directly or indirectly; for instance, by lowering the number of prey.

The DCA ordination accounted for about 55% of the variation in species composition and abundance and revealed a clustering of fields, depending on site but not on crop. That the clustering pattern was so clearly related to site, even if the dominant species were found at two or all of them, was interesting. It indicated that factors outside the fields themselves had been important in forming the spider communities studied.

Considering the relatively high severity and frequency of disturbance in these crops, it is not surprising that the main factors governing the community structure appeared to be in the surrounding environments of the cropped fields on each site. An example reflecting this may be the high numbers of *E. atra* and *E. dentipalpis* in the cereal fields at site C (Table 2), where the surrounding leys must have influenced the fauna. The high proportion of perennial ley in the crop rotation, in addition to leys and pasture in the adjacent area, may have been favorable for the *Erigone* species, thereby also increasing their number in the cereal fields. *Erigone* spp. can alternate between using and not using webs for capturing prey (Alderweireldt 1994), a strategy that is more successful in leys where cutting and grazing may favor species that have various prey strategies. Both species are found in perennial and annual crops, but often at a higher density in perennial crops (Schmidt & Tscharntke 2005). It is commonly reported that surrounding habitats and a heterogeneous landscape, including perennial crops, are important sources of aerial immigration to newly planted crops (e.g., Sunderland & Samu 2000; Öberg et al. 2007).

In summary, this study indicates that even very young perennial leys (17 months) constitute a better habitat for spiders than do undersown cereal fields. The use of multispecies crops undersown in cereals tends to result in a greater diversity of spiders than when the undersown crop consists of only one species. The clustering of sites, rather than of crops, in the ordination of the spider communities, confirms that factors outside the agricultural fields influence the spider fauna. Crops, subcrops, and the surrounding environs all seem to affect the diversity and density of spiders in cropped fields.

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