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Short- and longer-term colonization of alfalfa by spiders – a case study into the succession of perennial fields

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Abstract
We studied the short- and longer-term colonization of newly planted alfalfa fields in Nagykovácsi, Hungary, applying suction sampling as the means of collecting spiders. In the short-term experiment spider colonization was monitored over a season on 20 sampling occasions at 4 different distances (5–120 m) from the field edge, adjacent to a mature alfalfa field. The cumulative build-up of species richness showed equal rates everywhere on the field as the season progressed, suggesting that the edge and the middle of the field received an equal "propagule" load of species. However, spatio-temporal patterns – records of spiders at given positions and dates – indicated that close to the field edge the yearly catch of spiders was twice as many as in the middle of the field, with a smooth gradient observable between these end-points, and that per date species richness was also higher at the edge. Longer-term succession was studied in a different experiment, also starting from newly planted alfalfa. Lasting for 6 years, we monitored spiders by collecting them on six comparable occasions in each year, except for year 5. During this successional process we observed a maximum curve of both species and specimen numbers. In this hump-shaped time-series the spider population increased in species number and population density during the first 3 years, but showed a weak but pronounced decline afterwards. This tendency was also reflected in the trajectory the spider community followed in the ordination space and could not be attributed to yearly weather. We might speculate that ageing alfalfa is becoming less suitable for agrobionts over time, while this early stage of oldfield succession might not provide a suitable habitat for most natural spider species. In conclusion, while early steps of the succession are fast, the highest density and most typical agricultural community needs 3–4 years to build up. Perennial fields are therefore important elements of an agricultural landscape, because with time they become richer source habitats for the colonization of annual or newly planted perennial fields.

INTRODUCTION

Spider communities of arable crops are becoming well known in Europe, as a result of extensive research programs of the past decades (Luczak 1979; Toth & Kiss 1999; Samu & Szinetár 2002; Nyffeler & Sunderland 2003; Clough et al. 2005; Schmidt & Tscharntke 2005a; Oberg 2007). It is also becoming clear, that the existence of agricultural communities is based on meta-population processes (Topping & Sunderland 1994; Thomas & Jepson 1997; Thorbek et al. 2004). Harvesting and soil disturbance, such as ploughing, disrupts the life cycle of spiders, which either die or disperse during these perturbations (Thorbek & Bilde 2004). These vacated habitats become repopulated during autumn and spring (Bishop & Riechert 1990; Schmidt &

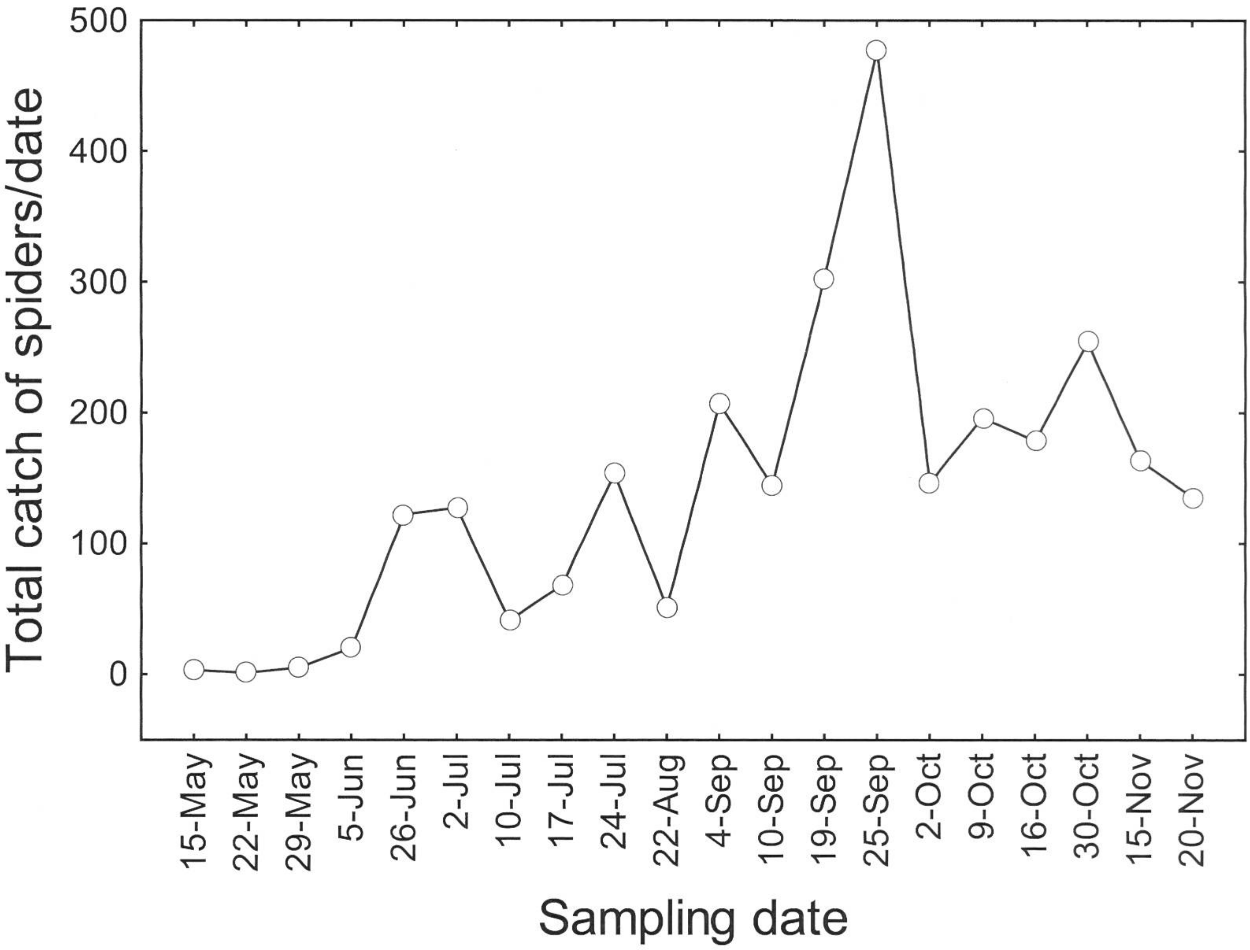

Fig. 1. Total number of spider individuals caught over the season in the newly planted "short-term study" alfalfa field.

Tscharntke 2005b), from source habitats. Spider communities in natural habitat patches can be sources of donor spider populations if species composition is sufficiently similar to the potential species composition of arable fields. This is usually fulfilled, if the vegetation structure is not very different (Kajak & Lukasiewicz 1994; Samu et al. 1999). Forested and bushy areas have very little interactions with arable fields, while grasslands overlap more in the composition of their spider communities. Perennial crops, like alfalfa – being arable crops themselves – show very high similarity with annual crops, and if they are managed less intensively they might build up very dense spider populations. In predominantly agricultural landscapes the area, position, age and management of perennial fields can be therefore a key factor in the natural enemy supply of more intensively managed annual fields (Sunderland & Samu 2000). In the present study we aimed to examine the process whereby spider populations build up in alfalfa fields. In a short-term study we followed how spiders penetrate from the edge into the field during its first year after sawing. In a longer-term study we monitored the spider community in an alfalfa field for six years, and detected changes in spider density and diversity over the period.

MATERIAL AND METHODS

Fields in the study were located in the experimental area of the Plant Protection Institute, Nagykovácsi, at the NW border of Budapest. Both alfalfa fields were managed without pesticide use. They were mowed 3 times/year.

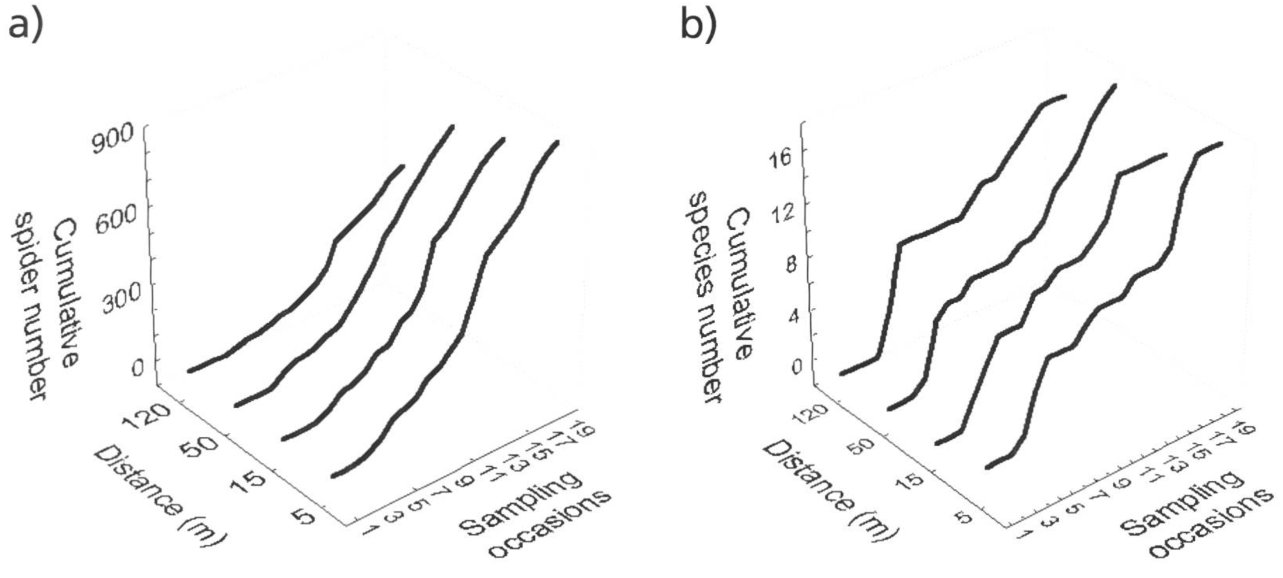

Fig. 2. Cumulative number of spiders (a) and of species (b) caught over the season at different distances from field edge.

The short term experiment was conducted on a nearby 7.5 ha (250 x 300 m) alfalfa field (47° 33′ 1.54″N, 18° 55′ 50.24″E). The field was sown in April 2001. In this year the field had a joint border with a 3 years old alfalfa field (other bordering habitats were: paved road, oldfield meadow and forest). We monitored immigration into the field by suction sampling in transects. Transects were positioned in the newly planted field parallel to its common border with the 3 years old alfalfa field. Transects were at 5, 15, 50 and 120 m from the border, and sideways separated by ca 100 m from field edges. Sampling method was identical to the long term study, except that a sample along a given transect consisted of 5 subsamples. Samples were taken at 7–10 days intervals, which resulted in 20 sampling occasions between 15 May and 20 November 2001.

The long term experiment was conducted on a 1.5 ha field (47° 32′ 51.85″N, 18° 55′ 56.94″E), bordered by other experimental fields on two sides, paved area on the third side and a dust road separating it from an oldfield meadow on the fourth side. The field was sown in April 1995, and its monitoring started 8 May 1995. We regularly sampled spiders for six years, until 2000, with the exception of 1999, when no sampling occurred. Yearly monitoring covered the season roughly the same way in each year, with one early sampling occasion in the period February–April, then from May until August one sampling occasion in each month, then a final autumn sampling in the period September–October, which amounts to six samples/year. Spiders were collected with a hand-held motorised suction sampling device (Samu & Sárospataki 1995; Samu et al. 1997). Each sample consisted of 10 subsamples taken in a transect at the approximate centre of the field, one subsample consisted of 10 press downs of the device (0.01 m^2 area covered by the suction tube).

The collected material was processed with standard techniques: after separation from suction trap material, spiders were stored in 70% ethanol, determined with stereo microscope using European keys (Heimer & Nentwig 1991; Roberts 1995). Taxonomic nomenclature followed Platnick's internet catalogue (Platnick 2008). Under "agrobionts" we refer concretely to 5 core agrobiont species: *Pardosa agrestis* (Westring, 1861), *Meioneta rurestris* (C. L. Koch, 1836), *Oedothorax apicatus* (Black-

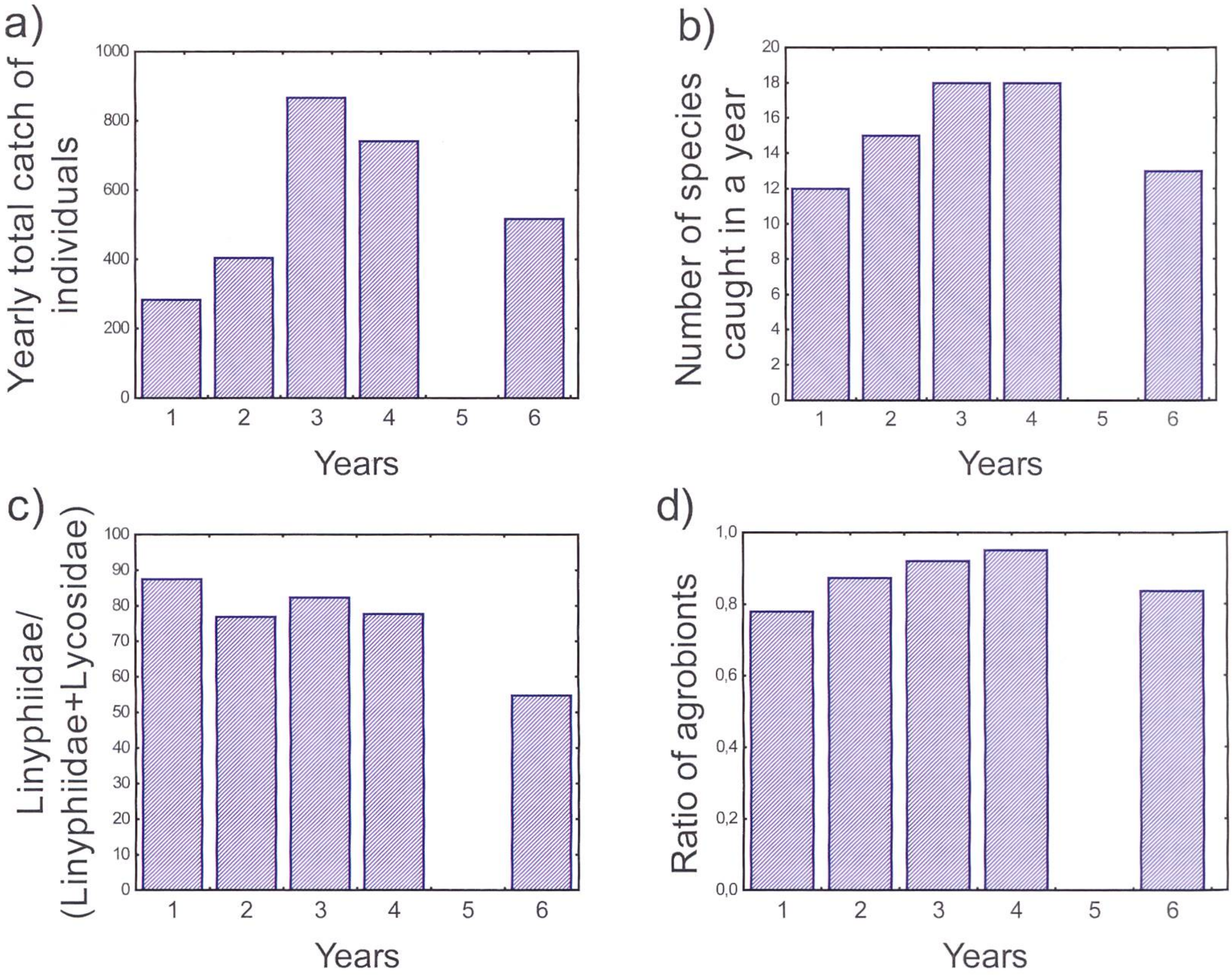

Fig. 3. Yearly changes of the spider assemblage in the alfalfa field of the "longer-term" experiment. a) number of spider individuals caught; b) number of spider species caught; c) The ratio of Linyphiidae within the Linyphiidae + Lycosidae complex; d) The ratio of individuals belonging to agrobiont species within the whole spider assemblage.

wall, 1850), *Pachygnatha degeeri* Sundevall, 1830, *Erigone dentipalpis* (Wider, 1834), which according to the national database can be regarded as the most typical and dominant species of Hungarian arable fields (Samu & Szinetár 2002).

RESULTS

During the studies we collected all together 7534 spiders from two nearby alfalfa fields, of which only ca 25% was adult. The specimens belonged to 53 species. The list of species by study field is given in the Appendix.

Short term colonization of a field by spiders

The total number of spider individuals caught increased with some fluctuation over the whole season (Fig. 1), with a strong peak in the second half of September. This peak was clearly attributable to the mass occurrence of juvenile linyphiids and the single species *Meioneta rurestris* (C. L. Koch, 1836). After having controlled for the seasonal variation, the effect of distance was highly significant (ln(x+1) transformation, $F_{1, 59}=38.03$, $P<0.0001$). The higher increase of spider numbers close to the field edge as opposed to towards the middle of the field is best visualised by the cumulative increase of spider catches (Fig. 2). This gives us the figures that, while at 5 m from the field edge we could catch 872 spider individuals over the whole season, towards the middle spider catches decreased continuously, and when reaching the centre catches halved (444 spider individuals).

Inspecting the cumulative number of species at the four different distances, we see no direct evidence that species numbers would be different; indeed the final numbers 17, 14, 17, 14 (at 5, 15, 51 an 120 m respective distances) suggest no difference. Statistical analysis of number of species, after controlling for date (treated as ordinal variable), showed a slight but significant decrease towards the middle of the field ($F_{1, 53}$=8.41, P<0.01).

While overall spider density and species richness decreased towards midfield, we also wanted to see, whether the two main families Linyphiidae and Lycosidae take their share equally in this trend. We computed a linyphiid : lycosid ratio (= Linyphiidae/(Linyphiidae + Lycosidae). This ratio showed a marked increase with date ($F_{19, 49}$=6.05, P<0.0001) and towards the middle of the field ($F_{1, 49}$=7.32, P<0.009). On the other hand, the ratio of agrobionts to all spiders did not show a similar change, it was even across time ($F_{17, 47}$=1.44, N.S.) and position within field ($F_{1, 47}$=1.34, N.S.).

Longer-term colonization of a field by spiders

In the longer-term study we intended to examine the temporal pattern that could be found in the same basic spider community variables that we investigated in the short-term study. Number of spider individuals caught tripled during the first 3 years, and showed a moderate decrease during the remaining years (Fig. 3a). Species numbers, although logically in a scaled-down way, also followed this pattern, with peak species number occurring in years 3–4 (Fig. 3b). The ratio of agrobionts followed the same hump-shaped pattern (Fig. 3d). Linyphiid spiders, the most common group, however, was gradually loosing its dominance against the second largest group, lycosids (Fig. 3c). We checked, whether the patterns in our variables were correlated with weather conditions in the given years, by correlating the variables with Pálfai Aridity Index (for year i PAI_i = [mean temperature($April_i$..$August_i$)]/[mean precipitation($October_{i-1}$..$August_i$]). Only Linyphiid ratio showed a marginally significant negative correlation, which after applying Bonferroni adjustment proved to be non significant.

This overall pattern of "present all along the study period and being the most numerous in year 3–4" was followed by a number of species: *Erigone dentipalpis* (Wider, 1834), *Meioneta rurestris* (C. L. Koch, 1836), *Pardosa agrestis* (Westring, 1861), *Pachygnatha degeeri* Sundevall, 1830. In contrast to the general trend, some species were present only in the early years (years 1–2): *Porrhomma microphthalmum* (O. P.-Cambridge, 1871), *Mangora acalypha* (Walckenaer, 1802), *Robertus arundineti* (O. P.-Cambridge, 1871); while other species were present in the late phase of the succession of the alfalfa field (years 4–6): *Pisaura mirabilis* (Clerck, 1757), *Tallusia vindobonensis* (Kulczynski, 1898), *Tibellus oblongus* (Walckenaer, 1802). Typically these latter species were specific to the long-term study, and absent from samples from the short-term study field. During the succession of the alfalfa field, changes in the overall composition of the spider community were detectable by ordination analysis. The applied Bray-Curtis Ordination analysis also suggests that community processes had a transition from one stage to another, but these were not linear, rather they took different directions during the different phases of the succession (Fig. 4).

DISCUSSION

The short- and longer-term studies together draw a picture of the spatio-temporal processes of how perennial arable fields get populated by spiders after their establishment. Ploughing and sowing a field clearly disrupts the spider population, which must

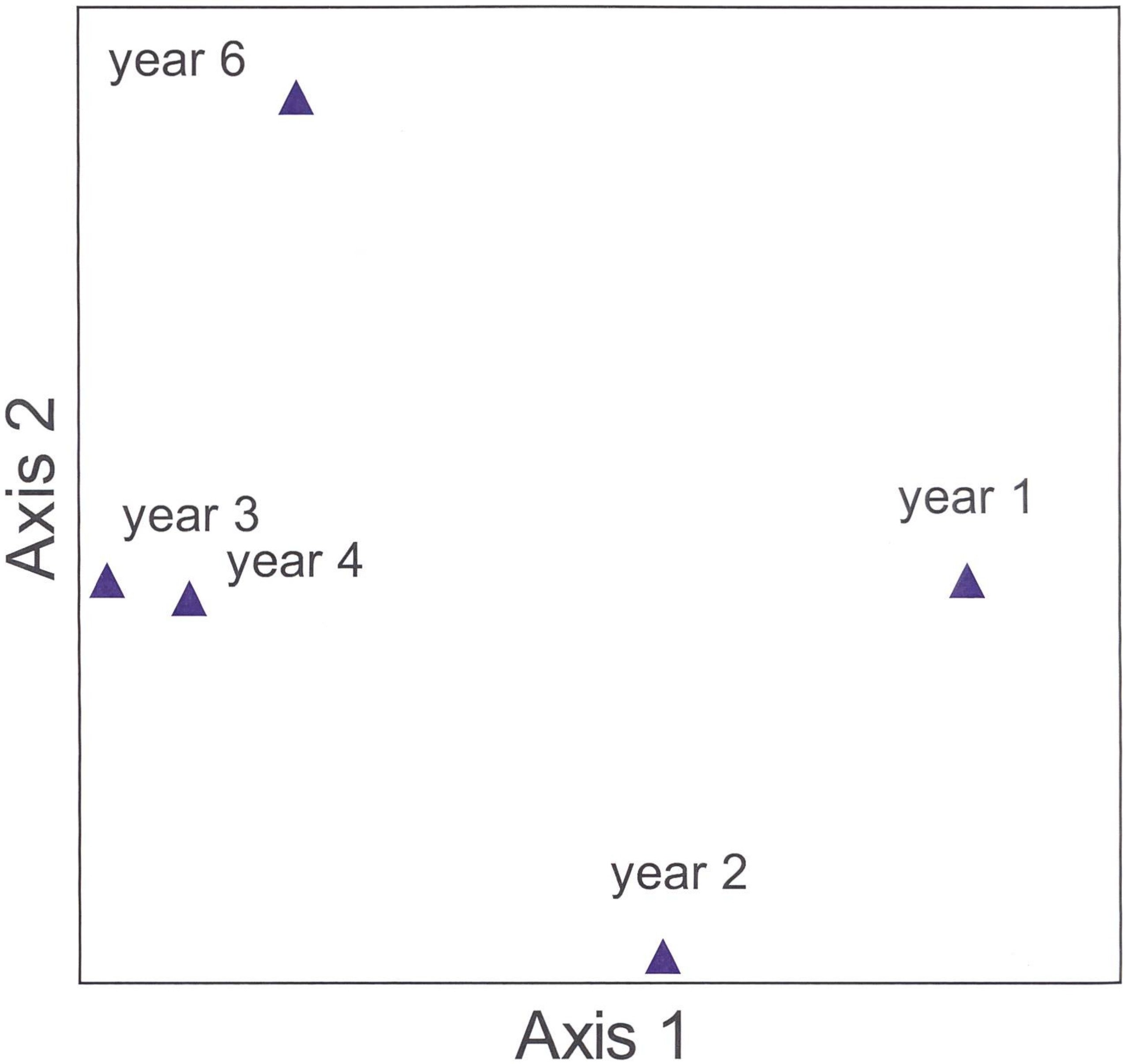

Fig. 4. Bray-Curtis Ordination of the spider community in the given years of the "longer-term" study. In the ordination analysis done by PC-Ord 4.0 (McCune & Mefford 1999) the relative Sorensen distance measure was used. The 1st axis represented 81.17%, the 2nd axis 8.92% of the variance.

then virtually start from zero. This has already been demonstrated experimentally with emergence traps (Thorbek & Bilde 2004), and the near zero catches at the beginning of the present short-term study also corroborate those results. The short-term study revealed that from this starting point the build up of the spider population occurs both through the advancement of the season and spatially from the edge into the middle of the field. The numerical increase of the spiders was quite steady until late autumn, with one outlying peak, that was due to the mass occurrence of juvenile Liniphiidae. Similarly to other studies that compared arthropod communities close to field edges and in the centre of the field (Kromp & Steinberger 1992; Alderweireldt 1993), we also found a spatially strong gradient of spider density decreasing towards midfield. However, this pattern was less clearly repeated in species numbers. One can speculate, that this is because many species are represented with few individuals (nearly half of the species were singletons in the short-term study). These species are likely to be aerial immigrants, that – at least in this early successional phase – cannot establish a population, and can be viewed as tourists. Such aerial immigrants are likely to hit the field at random locations, which then might cause the even distribution of species numbers. On the other hand, immigrants that arrive on foot come from the nearby agricultural area, and represent a more limited, but more suitable set of species. The slow spread of cursorial species is underlined by the finding that Linyphiidae/Lycosidae ratios were higher towards the middle of the field, a pattern that was found in other studies that compared field edges to field centre (Sunderland 1987; Klimes 1989; Maelfait & de Keer 1990; Nyffeler & Breene 1992). The longer-term study revealed that lycosid populations were only able to catch up over years. From year 1 to 6 there was a 600% increase in lycosids, while in linyphiids only some 30% increase. A very similar trend was found both in overall spider abundance and Linyphiidae/Lycosidae ratio in a Swiss study, where the succession of a meadow was investigated (Nentwig 1988).

The longer-term study revealed that the increase of the spider population of the alfalfa field does not end after one year; on the contrary, spider abundance nearly doubled every year during the first three years. With the maturation of the alfalfa field, species numbers found per year increased during the first three years, and at the same time the ratio of agrobionts increased to 95%. This supports earlier findings, that arable communities are distinct entities, that can be described by the overall dominance of agrobiont species (Samu & Szinetár 2002). Even small fields with diverse habitat surroundings "select" agrobionts from a very broad species pool (Szinetár et al. 2006). The present study shows, that over the first few years of succession of perennial fields these communities reach a climax stage, with 95% of the individuals agrobionts and overall high spider density. Year 6 produced lower abundance and species richness values in the study. Unfortunately the value for this year greatly influences how trends in the second half of the successional occurrences are judged. Changes in the community structure, and also the lack of correlation with yearly weather suggest that year 6 is not an outlier, and that there is a genuine change in the population trends of spiders after year 3. Alfalfa fields age quickly after 3 to 4 years, and get invaded by grasses. This causes the volume of the vegetation to be lower, more sparse. If alfalfa fields are left alone they convert into meadows. Thus occurrences in years 4–6 should be viewed in our opinion as a transitional stage with a stagnation or decrease of the agricultural spider community, which is likely to change even more when the transition into the meadow state occurs.

In conclusion, it can be told that there is a pronounced and characteristic build-up of spider populations and the whole spider community that takes place after the establishment of a perennial arable field. This succession is marked by a steep and long-lasting increase of spider abundance. Not only aerial, but cursorial immigrants from neighbouring fields also play an important role in this, as population build-up was more advanced at the field edge all along the first year of succession. Three to four years are needed for the spider community to reach its climax state and maximal abundance. This underlines the importance of perennial fields, because these harbour high quality and abundant source communities, from which spiders can invade annual fields in the landscape.

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APPENDIX

Total catch of spider individuals that were determined to species in the "long-term study" alfalfa field and in the "short-term study" alfalfa field collected by suction sampling with the sampling effort detailed in Material and Methods.

Family	Species	Long-term study	Short-term study
Araneidae	*Hypsosinga pygmaea* (Sundevall, 1832)	4	1
Araneidae	*Mangora acalypha* (Walckenaer, 1802)	7	6
Dictynidae	*Argenna subnigra* (O. P.-Cambridge, 1861)	4	
Gnaphosidae	*Haplodrassus minor* (O. P.-Cambridge, 1879)		1
Gnaphosidae	*Haplodrassus signifer* (C. L. Koch, 1839)	1	
Gnaphosidae	*Zelotes gracilis* Canestrini, 1868	2	
Hahniidae	*Hahnia nava* (Blackwall, 1841)		1
Linyphiidae	*Araeoncus humilis* (Blackwall, 1841)	21	19
Linyphiidae	*Bathyphantes gracilis* (Blackwall, 1841)	3	1
Linyphiidae	*Centromerus sylvaticus* (Blackwall, 1841)	1	
Linyphiidae	*Ceratinella brevipes* (Westring, 1851)	1	
Linyphiidae	*Ceratinella brevis* (Wider, 1834)	1	
Linyphiidae	*Diplocephalus cristatus* (Blackwall, 1833)	1	
Linyphiidae	*Diplostyla concolor* (Wider, 1834)	3	
Linyphiidae	*Erigone dentigera* O. P.-Cambridge, 1874	1	
Linyphiidae	*Erigone dentipalpis* (Wider, 1834)	258	34
Linyphiidae	*Mecopisthes peusi* Wunderlich, 1972		28
Linyphiidae	*Meioneta rurestris* (C. L. Koch, 1836)	334	906
Linyphiidae	*Meioneta simplicitarsis* (Simon, 1884)	15	19
Linyphiidae	*Micrargus subaequalis* (Westring, 1851)	1	
Linyphiidae	*Microlinyphia pusilla* (Sundevall, 1830)	1	
Linyphiidae	*Oedothorax apicatus* (Blackwall, 1850)	85	6
Linyphiidae	*Porrhomma microphthalmum* (O. P.-Cambridge, 1871)	7	7
Linyphiidae	*Silometopus reussi* (Thorell, 1871)	3	1
Linyphiidae	*Stemonyphantes lineatus* (Linnaeus, 1758)	1	
Linyphiidae	*Syedra gracilis* (Menge, 1869)		8
Linyphiidae	*Tallusia vindobonensis* (Kulczynski, 1898)	3	
Linyphiidae	*Tenuiphantes flavipes* (Blackwall, 1854)	1	
Linyphiidae	*Tenuiphantes tenuis* (Blackwall, 1852)	2	8
Linyphiidae	*Trichoncoides piscator* (Simon, 1884)	2	1
Liocranidae	*Phrurolithus festivus* (C. L. Koch, 1835)	1	
Lycosidae	*Aulonia albimana* (Walckenaer, 1805)	1	
Lycosidae	*Pardosa agrestis* (Westring, 1861)	58	19
Lycosidae	*Pardosa hortensis* (Thorell, 1872)	2	
Lycosidae	*Pardosa prativaga* (L. Koch, 1870)	4	
Lycosidae	*Xerolycosa miniata* (C. L. Koch, 1834)	1	
Philodromidae	*Thanatus striatus* C. L. Koch, 1845	1	
Philodromidae	*Tibellus oblongus* (Walckenaer, 1802)	29	1

Family	Species	Long-term study	Short-term study
Pisauridae	*Pisaura mirabilis* (Clerck, 1757)	7	
Salticidae	*Heliophanus cupreus* (Walckenaer, 1802)	1	
Tetragnathidae	*Pachygnatha degeeri* Sundevall, 1830	39	11
Theridiidae	*Enoplognatha thoracica* (Hahn, 1833)	1	1
Theridiidae	*Neottiura bimaculata* (Linnaeus, 1767)	2	
Theridiidae	*Robertus arundineti* (O. P.-Cambridge, 1871)	6	
Theridiidae	*Robertus lividus* (Blackwall, 1836)	1	
Theridiidae	*Steatoda phalerata* (Panzer, 1801)		1
Theridiidae	*Theridion impressum* L. Koch, 1881		6
Thomisidae	*Ozyptila atomaria* (Panzer, 1801)		1
Thomisidae	*Ozyptila scabricula* (Westring, 1851)		1
Thomisidae	*Thomisus onustus* Walckenaer, 1806	1	
Thomisidae	*Xysticus kochi* Thorell, 1872		1
Zoridae	*Zora parallela* Simon, 1878	1	
	Total (individuals determined to species)	919	1093
	Total (all individuals)	5650	1884
	Number of species	43	26