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Landscape effects on recolonisation patterns of spiders in arable fields

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Abstract

The influence of the availability of surrounding boundaries and grasslands on the recolonisation of lycosid and linyphild spiders was studied in early spring in 12 winter barley fields situated in differently structured landscapes. It was found that the more cursorial lycosid spiders foremost showed a dependence on time when recolonising arable fields, and increased in numbers during the critical time of pest establishment, although lycosid species richness also was related to the surrounding landscape. Linyphild spiders, which are more likely to disperse by air than lycosids, did not show an increase in numbers over time, but were more affected by the surrounding landscape. However, these spiders also showed a dependence on time, because the positive effect of surrounding boundaries was significant in the beginning but not at the end of the study period. Thus, most spiders showed a difference in migration patterns over time and both spider families were positively influenced by the surrounding boundaries and grasslands during recolonisation of crop fields after winter. In order to enhance pest suppression by spiders, overwintering structures should be provided in crop-dominated landscapes to facilitate spider migration into crop fields during early spring. © 2007 Elsevier B.V. All rights reserved.

Keywords: Araneae; Boundaries; Grassland; Linyphiidae; Lycosidae; Migration; Pest management; Spatial ecology; Winter barley

1. Introduction

Availability and quality of hibernation sites are a limiting factor for invertebrate conservation and biological control in agricultural landscapes (Pywell et al., 2005). High abundance of spiders in non-crop habitats during winter and spring suggest that these habitats are more appropriate for overwintering than annual crop fields and an important source for immigration (Luczak, 1979; Marc et al., 1999; Pfiffner and Luka, 2000; Lemke and Poehling, 2002). Schmidt and Tscharntke (2005b) showed that spider communities in crops were composed mainly of species that had higher abundances in perennial habitats during spring. Consequently, even for species that have high densities in annual crop fields a variety of crops and perennial habitats should be better than arable crops alone. The degree to which natural enemies will be effective in controlling pests in annual crop fields depends partly on the quality and quantity of overwintering sites (Wissinger, 1997). Östman et al. (2001) showed that a high perimeter to area ratio and high proportions of non-crop habitats were positively related to the strength of predator impact on aphid establishment in spring sown cereals early in spring. Hence, if predators are to be present in crop fields during pest establishment, immigration from other habitats is necessary. Spiders disperse either by moving on the ground from nearby habitats or by air (aeronautic behaviour on silken threads known as ballooning) from nearby habitats or from more remote habitats (Marc et al., 1999).

The spider families Lycosidae and Linyphiidae (Araneae) are common on arable land in Central and Northwestern Europe (Toft, 1989; Feber et al., 1998; Samu and Szinetár,

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2002; Pfiffner and Luka, 2003; Clough et al., 2005; Öberg and Ekbom, 2006) and they are known to have an impact on common insect pests such as aphids (Luczak, 1979; Nyffeler and Benz, 1987; Mansour and Heimbach, 1993; Lang, 2003). Different kinds of gut content analyses have also detected remains of aphids in these predators when caught in barley fields (Chiverton, 1987; A.-K. Kuusk, personal communication).

The aim of this study was to investigate and compare the influence of the availability of surrounding hibernation sites on the recolonisation of arable fields by lycosid and linyphild spiders at consecutive time intervals during early spring recolonisation. To our knowledge, this is the first study on landscape effects on early spring colonisation of spiders to arable land, which is highly important for an efficient natural pest control. The following questions were asked:

- Do lycosid and linyphild spiders recolonise winter sown arable fields in early spring?
- Does the structure of the surrounding landscape influence lycosid and linyphild recolonisation patterns?
- Are lycosids and linyphilds differently affected by landscape during recolonisation?

An important difference between the two families is their respective modes of dispersal; Linyphiidae constitutes a high proportion of aeronauts over agroecosystems, and lycosid spiders move mainly by walking (Luczak, 1979; Weyman et al., 2002). Therefore, it was hypothesised that lycosid abundance in barley fields would be more likely to show a slow but continuous increase in the field compared with the linyphiids due to their different modes of dispersal. Linyphiids might recolonise more quickly and in higher numbers at a time due to their ballooning behaviour, whereas the recolonisation of lycosids might be a more continuous process with some individuals arriving later because they had to walk from places farther away. It was also suggested that the impact of landscape factors on recolonisation patterns might depend on the dispersal ability of the spiders. Linyphiid spiders would be affected earlier by the surrounding landscape than lycosids as linyphiids might immediately recolonise from more distant hibernation sites due to their ballooning behaviour. In contrast, landscape effect might be continuous but increasing in importance or occurring only later in spring for lycosids.

2. Materials and methods

The study was conducted in 12 agricultural landscapes in the low mountain ranges of Central Hesse, Germany. The total area of the study region covered about 700 km^2 . The agricultural system is predominantly low-input with small field sizes. The landscape is dominated by forest (48.0% total cover), agricultural systems (16.6% total cover), and managed grassland (17.7% total cover). Mean annual temperature ranged from 7 to 9 °C, mean annual precipitation varied from 650 to 1100 mm (Hessisches Landesamt für Umwelt und Geologie, 2005). The selected landscapes were delimited by circles of 500 m in radius and were non-overlapping. The landscapes strongly differed in their availability of overwintering habitat for spiders (i.e. field boundaries, perennial grasslands, forest) and ranged from highly heterogeneous land-use with high cover of grassland/forest and high edge density to more homogeneous land-use with high cover of arable land and low edge density (Table 1). The landscapes were scattered over the whole study region. Mantel tests (based on Spearman correlations, 1000 permutations) were performed to relate geographic distance of the landscapes to the measure of availability of overwintering sites (see Section 2.2). No spatial autocorrelation was found (r = 0.18), p = 0.11). Single study sites, which were located in the centres of the landscapes, were conventionally managed winter sown barley fields with a range in size between 0.9 and 3.3 ha (mean 1.6 ha). The elevation of the study sites varied from 170 to 505 m a.s.l. Variation in management was quantified by using questionnaires completed by the farmers. Total application of nitrogen during the year (range from 90 to 140 kg/ha/year) and number of plant protection applications

Table 1

Total length of boundaries and cover of grassland and forest in the 500 m radius circles and species richness of Lycosidae and Linyphiidae during the whole study period for each study site

Field	Length of boundaries (km)	Grassland (%)	Forest (%)	No. of lycosid species	No. of linyphiid species
AL	23.8	24.9	0.9	7	11
BH	26.1	43.5	16.3	8	18
DH	17.6	20.9	22.2	7	11
EH	21.5	30.3	2.6	3	11
FH	17.4	17.1	35.9	6	16
MO	15.7	0.2	0.0	4	10
NW	23.5	7.1	2.3	7	15
RH	24.3	21.2	23.2	6	17
SB	22.2	10.3	5.7	8	12
SH	29.4	36.6	1.8	9	13
WB	25.8	41.0	10.6	9	15
WH	21.8	6.2	10.9	10	13

(herbicides, fungicides, and growth regulators) during the study period (range from 1 to 3 occasions) was recorded for all study sites. No insecticides were applied on the fields during the study period.

2.1. Sampling and species determination

Spiders were sampled using pitfall traps (diameter: 85 mm, volume: 500 ml). Traps were filled with approximately 100 ml of saturated NaCl-solution with a detergent added to reduce surface tension. Each trap was shielded by a $25 \text{ cm} \times 25 \text{ cm}$ acrylic glass pane at a height of about 10 cm to avoid flooding by rain. Altogether, 10 traps were placed in three diagonal lines evenly distributed across each sampling site and were emptied every three days between 22 March and 9 May in 2004. All collected lycosids and linyphilds were counted and adults were determined to species (nomenclature following Platnick, 2006). Spiders were identified using Roberts (1987, 1995) and Heimer and Nentwig (1991). To obtain species richness and activity density for each site, the 10 traps were pooled for each site for every sampling period.

Reservations about pitfall traps have been raised in the literature, because they may not reflect the true abundance or even reflect a change in density of arthropods (Topping and Sunderland, 1992). However, lycosid spiders are most effectively collected with pitfall traps and it has been shown that the number of linyphild species caught is about the same in pitfall traps as in D-vac trapping (Dinter, 1995; Standen, 2000). Also, one of our aims was to study the colonisation of predators and pitfall traps have been shown to be suitable for monitoring activity (Bishop and Riechert, 1990). Pitfall traps can also be suitable for comparisons within the same habitat (Topping and Sunderland, 1992), which is the case in the present study. Therefore, pitfall traps are a good choice for comparing spider catches among sites compared with alternative methods.

Sampling periods had to be standardised because the differences in altitude and sun exposure of the sampling sites may influence microclimate which, in turn, may affect spider activity. Altitude of the study sites were determined using ArcView 3.2 GIS software (ESRI, Redlands, CA). Mini-max thermometers were buried in the soil at a depth of 2 cm. Minimum and maximum temperatures were measured for each sampling period. The start of blooming for Taraxacum officinale adjacent to the sampling sites was recorded at each sampling site. The time for blooming was correlated with altitude (r = 0.72, p = 0.009) and mean minimum soil temperature (r = -0.64, p = 0.024) of the study sites. Therefore, this attribute was used to eliminate bias caused by the climatic variance of study sites. Duelli et al. (1999) proposed standardisation of sampling units in terms of T. officinale flowering to compare findings in different years. Schweiger et al. (2005) also corrected for climatic differences between countries with the blooming date of T. officinale. To compare sampling periods in the present study, sampling days were defined as days before/after blooming of *T. officinale*. After standardisation of sampling periods, a time span of 18 days before until 18 days after start of *T. officinale* bloom remained for comparison of the study sites. To minimize the fluctuations in the numbers of spider individuals caused by the short sampling periods of three days, four sampling periods were included in each of three sampling phases.

2.2. Landscape analyses

Landscape parameters such as cover of land-use types and edge length were calculated using ArcView 3.2 GIS software (ESRI), based on a digital map of land use derived from aerial photographs of 2002 and updated by field survey in 2004. In order to evaluate the landscapes surrounding the cereal fields in terms of availability of overwintering habitats for spiders, the length of field boundaries within a 500 m radius were calculated. Five hundred meters has been shown to be a suitable scale for studying spiders (Schmidt and Tscharntke, 2005a). Within the studied region, only fields of different land-use (e.g. annual/perennial; crop/non-crop) can provide semi-natural boundary habitats and structures suitable for spider hibernation. Those boundaries usually resemble grassland-strips, but also banks, edges of groves or shrubbery, or forest edges. No such structures existed between directly adjacent fields of annual crops. Therefore, all edges were removed between similar land-use types from the digital map by dissolving the borderlines between polygons of equal land use. The total length of the remaining boundaries reflects the heterogeneity of land use within the landscapes, and provides an estimate of mosaic structure or fragmentation. Also, the length of boundaries was positively correlated with the cover of grassland in the surrounding landscape (r = 0.66,p = 0.019, n = 12). Therefore, only length of boundaries was used as a surrogate for the availability of refuge and hibernation sites for spiders in the surrounding landscapes.

2.3. Data analyses

This study focuses on the spider families Lycosidae and Linyphiidae. In addition to analysing activity densities of the families, single species with high activity densities were also analysed separately in order to see if they show different patterns than the total family together. A species had to represent at least 10% of the total adult specimens caught for each family and be present in at least 9 out of 10 fields in order to be analysed separately. Species richness of Lycosidae and Linyphiidae, respectively, were also used as dependent variables in the analyses.

Total application of nitrogen during the year and number of plant protection applications during the study period were analysed in relation to spider activity densities and species richness for the whole study period in a general linear model with number of plant protection applications (1–3) as a class variable and fertilisation (N [kg/ha/year]) as a continuous variable. Fertilisation and plant protection applications did not explain any of the variation in spider activity densities and species richness among the different study sites. Therefore, the analysis continued without further consideration of these management factors.

The recolonisation pattern was studied by comparing different phases. The effect of phase on activity densities and species richness was analysed using a repeated measurement analysis of variance in procedure MIXED in SAS to test for differences in time (n = 3) with fields as replicates (n = 12),

with compound symmetry as covariance structure based on Akaike information criterion (AIC). To test whether landscape effects on recolonisation depend on the time of observation, the effect of the total length of boundaries in the surrounding landscape on the activity density and species richness of spiders was analysed using a linear regression for each phase. Data were log-transformed prior to statistical analysis whenever necessary. Statistical analyses were performed in SAS 8 for Windows.

Table 2

Total activity density of fycosid and impenite species captured on 12 white sown barley helds and activity density after standardisation by bloom of 1. off	fficir	inc	ai
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	Total	After standardisa		
		Phase 1	Phase 2	Phase 3
Lycosidae	1834	216	396	1096
Pardosa amentata (Clerck)	324	0	24	286
Pardosa agrestis (Westring)	245	0	16	215
Trochosa ruricola (De Geer)	219	82	80	45
Pardosa pullata (Clerck)	157	0	15	133
Pardosa palustris (Linnaeus)	144	0	13	115
Trochosa terricola Thorell	30	4	9	15
Alopecosa pulverulenta (Clerck)	14	0	0	14
Hygrolycosa rubrofasciata (Ohlert)	11	4	3	4
Alopecosa cuneata (Clerck)	11	0	1	10
Pardosa hortensis (Thorell)	4	0	1	2
Pardosa lugubris (Walckenaer)	1	0	0	0
Aulonia albimana (Walckenaer)	1	0	1	0
Linyphiidae	2157	575	629	498
Oedothorax apicatus (Blackwall)	690	159	220	193
Erigone atra Blackwall	591	171	144	129
Meioneta rurestris (C. L. Koch)	230	73	80	36
Erigone dentipalpis (Wider)	190	39	56	62
Walckenaeria vigilax (Blackwall)	102	31	21	12
Walckenaeria dysderoides (Wider)	68	25	30	4
Bathyphantes gracilis (Blackwall)	55	14	18	15
Walckenaeria nudipalpis (Westring)	29	6	6	4
Porrhomma microphthalmum (O. PCambridge)	28	7	8	5
Dicymbium nigrum brevisetosum Locket	28	9	14	3
Erigonella hiemalis (Blackwall)	22	4	8	10
Araeoncus humilis (Blackwall)	21	1	5	6
Eperigone trilobata (Emerton)	13	9	0	3
Pelecopsis parallela (Wider)	8	1	1	0
Silometopus elegans (O. PCambridge)	6	1	0	2
Collinsia inerrans (O. PCambridge)	5	2	1	0
Jacksonella falconeri (Jackson)	5	2	3	0
Oedothorax fuscus (Blackwall)	4	1	2	1
Mioxena blanda (Simon)	4	3	0	0
Tapinocyba insecta (L. Koch)	4	0	1	2
Centromerita bicolor (Blackwall)	3	3	0	0
Troxochrus scabriculus (Westring)	3	3	0	0
Porrhomma oblitum (O. PCambridge)	2	1	1	0
Porrhomma errans (Blackwall)	2	1	0	1
Diplocentria bidentata (Emerton)	2	1	0	0
Stemonyphantes lineatus (Linnaeus)	2	0	1	0
Tenuiphantes zimmermanni (Bertkau)	2	0	2	0
Tenuiphantes tenuis (Blackwall)	2	1	0	1
Microlinyphia pusilla (Sundevall)	2	0	1	1
Centromerus serratus (O. PCambridge)	1	0	0	0
Tapinocyba praecox (O. PCambridge)	1	1	0	0
Gongylidiellum vivum (O. PCambridge)	1	0	0	1
Ceratinella brevis (Wider)	1	0	0	1
Diplostyla concolor (Wider)	1	0	0	0



Fig. 1. Mean activity density (S.E., n = 12) of lycosid spiders (adults and juveniles) in the different phases, where 1 is the first phase. Statistics are shown in the text.

3. Results

In total, 1834 lycosids (including 671 juveniles) belonging to 12 species and 2157 linyphilds (including 14 juveniles) belonging to 34 species were collected (Table 2). Other families collected were Tetragnathidae, Thomisidae, Theridiidae, Gnaphosidae, Hahniidae, and Pisauridae (23%, 2%, 0.6%, 0.5%, 0.09%, and 0.04% of total 5413 spider specimens collected, respectively), but were not considered further. After standardisation of the sampling periods, 1708 lycosids (including 614 juveniles) belonging to 32 species remained (Tables 1 and 2). The lycosid species *Pardosa amentata, Pardosa agrestis* and *Trochosa ruricola*,

and the linyphild species *Oedothorax apicatus*, *Erigone atra* and *Meioneta rurestris* were dominant species. As *Pardosa* spp. have their maturation during the studied time of year, species richness of Lycosidae and the two dominant *Pardosa* species were only included in the analysis of landscape effect and not in the analysis of temporal effect.

3.1. Lycosidae

Total activity density of Lycosidae (adults and juveniles) $(F_{2,33} = 12.87, p < 0.0001)$ increased significantly over time (Fig. 1). Activity density of *T. ruricola* showed no difference between phases.

Lycosid species richness was positively associated with total length of boundaries in the surrounding landscape in the second and third phase (Tables 1 and 3). Activity density of one of the dominant lycosid species, *T. ruricola*, was positively related to total boundaries in the landscape in all phases (Table 3). Activity density of all Lycosidae (adults and juveniles) and the two lycosid species *P. amentata* and *P. agrestis* showed no association with total boundaries in the surrounding landscape in any of the three phases (Table 3).

3.2. Linyphiidae

Activity density of Linyphiidae in total (adults and juveniles), linyphiid species richness, and the three dominant linyphiid species *O. apicatus*, *M. rurestris* and *E. atra* showed no difference between phases.

Table 3

Model statistics derived from linear regressions for activity density and species richness of Lycosidae and Linyphiidae, together with dominant species, against total length of boundaries in the surrounding landscape (circle of 500 m radius) in each phase

	Phase	р	$F_{1,10}$	R^2
Activity density of spider families and	l species			
Lycosidae	1,2,3	NS	_	-
Pardosa amentata	1,2,3	NS	_	-
Pardosa agrestis	1,2,3	NS	-	-
Trochosa ruricola	1	0.027	6.7	0.4011 (+)
	2	0.0012	20.19	0.6687 (+)
	3	0.0244	7.01	0.412 (+)
Linyphiidae	1	0.0169	8.2	0.4506 (+)
	2	NS	-	-
	3	NS	-	-
Oedothorax apicatus	1,2,3	NS	_	_
Erigone atra	1,2,3	NS	-	-
Meioneta rurestris	1	0.0096	10.18	0.5045 (+)
	2	0.0117	9.47	0.4864 (+)
	3	NS	-	-
Species richness				
Lycosidae	1	NS	_	-
-	2	0.0131	9.06	0.4753 (+)
	3	0.0494	5	0.3331 (+)
Linyphiidae	1,2,3	NS	-	-

Only statistics for significant differences are shown. n = 12 in all cases. NS: non-significant (p > 0.05). 1: first phase, 2: second phase, 3: third phase.

Activity density of all linyphiids was positively associated with total boundaries in the surrounding landscape in the first phase, but not in the second and third phase (Table 3). The dominant linyphiid species *M. rurestris* had higher activity density in sites with higher total boundaries in the landscape in the first and second phase. Activity density of the two linyphiid species *O. apicatus* and *E. atra*, and linyphiid species richness showed no association with total boundaries in the surrounding landscape in any of the three phases (Tables 1 and 3).

4. Discussion

Lycosids increased in the fields over time, indicating a recolonisation to the arable fields during spring, whereas linyphilds did not. On the other hand, Öberg and Ekbom (2006) found an increase of linvphilds in crop fields after spring sowing, but not of lycosids. However, in Öberg and Ekbom (2006) study, lycosids were not affected by the sowing procedure whereas sowing was detrimental for the activity density of linyphilds. A reason for not detecting a recolonisation of the linyphilds in the current study can be that they were present in the fields when the study started. The linyphilds might have overwintered in the fields, although several studies have found high abundances of spiders in adjacent semi-natural habitats and low abundances in crop fields during winter (Pfiffner and Luka, 2000; Lemke and Poehling, 2002; Schmidt and Tscharntke, 2005b). More likely is that they already had migrated from overwintering habitats, thus making the recolonisation into fields faster than for lycosids.

Linyphiid activity density in the cereal fields was, in contrast with lycosid activity density, related to the surrounding landscape. Activity density of linyphilds was positively associated with total length of boundaries in the landscape in the first of the three phases, but the landscape effect disappeared in the later phases. This might imply that surrounding boundaries and grasslands have an effect on early recolonisation of linyphiids, but not on the later migratory patterns. Schmidt and Tscharntke (2005a) also found that linyphiid abundance was higher in landscapes with larger proportions of non-crops in late spring, but that the landscape effect disappeared in early summer. They discuss that continued dispersal could have evened out the differences between landscapes in early summer or that linyphilds had approached maximum densities in the fields. These reasons can also explain the patterns in the current study. Several studies have showed that higher proportions of non-crops in the surrounding landscape increase the number of spiders, especially linyphilds, in cereal fields (Halley et al., 1996; Samu et al., 1999; Schmidt et al., 2005; Thorbek and Topping, 2005).

The number of lycosid species was positively associated with total length of boundaries in the landscape in the second and third phase. This might imply an effect of landscape on migration because some species associated with edge habitats move to the arable land later in spring and enhance species richness. However, the landscape effect on lycosid species richness might only have been detectable later in spring due to their maturation into adults during this time. Still, the landscape effect shows that fewer lycosid species arrived in crop fields in crop dominated landscapes, most likely because fewer species exist there. Nearby perennial habitats, such as boundaries, are structurally and vegetationally more diverse, which can lead to more species in crop fields, especially for species that are less adapted to arable dominated environments. Other studies also found that species richness of spiders increased with proportions of non-crops in the surrounding landscape (Clough et al., 2005; Schmidt et al., 2005). However, these studies included all trapped spider species, whereas the current study only found this result for lycosid species richness, and not for the number of linyphiid species.

As for the total number of linyphilds, none of the three dominant linyphiid species showed any increase over time in the crop fields. The surrounding landscape affected two of the common species under study. The lycosid T. ruricola, in contrast to its family, and the linyphild M. rurestris, in similarity with its family, were positively related to the total length of boundaries in the surrounding landscape. They did not show an increase in activity density over time. Thus, these species probably migrated quickly from overwintering habitats to arable fields after winter, becoming dominant species there, but their activity density in crop fields was positively influenced in landscapes with many non-crop habitats. Clough et al. (2005) found that T. ruricola was not related to the surrounding landscape in a study performed later in spring than the current study. Perhaps the influence of landscape on T. ruricola disappears later in spring/early summer. For M. rurestris, the landscape effect was not apparent in the last phase, thus, the species was only affected by surrounding non-crop habitats in the beginning and middle of the study, implying an effect of landscape on early migration. M. rurestris is able to balloon, whereas T. ruricola is mainly a cursorial disperser. This might explain why the landscape influences the linyphild species a shorter time earlier in the season than for the lycosid species. Clough et al. (2005) also found that *P. agrestis*, *P. amentata*, O. apicatus, and E. atra were not influenced by the surrounding landscape, which is in accordance with the current study. As these species were dominant in the fields and therefore seem to have a preference for arable land, perhaps they manage to locate crop fields irrespective of the surrounding landscape.

In conclusion, the more cursorial lycosid spiders were clearly recolonising arable fields, and increased in numbers during the time of pest establishment, but this was not influenced by landscape heterogeneity. The species richness of the lycosids was, on the other hand, positively associated with landscape heterogeneity. Hence, in landscapes with more available non-crop habitats, a higher number of lycosid species found their way to annual crop fields. The linyphilds did not show an increase in activity density or species richness over time, which can be explained by quick recolonisation after winter due to their ballooning behaviour. For these spiders, however, there was also an influence of time, because the effect of landscape was significant on activity density in the beginning but not at the end of the study. Accordingly, the number of linyphiid individuals caught in annual crop fields was higher in more diverse landscapes, even though the number of linyphild species was the same in the fields irrespective of the availability of noncrop habitats in the surrounding landscape. Several studies conducted in late spring or early summer have shown that a diverse landscape increases spider abundance and diversity in crops. In the present study, it has been shown that the recolonisation of spiders to cereal fields during the critical time in early spring appears to be, to some level, dependent on the conservation and enrichment of non-crop habitats in the surrounding landscape.

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