Spiders in the Agricultural Landscape

Diversity, Recolonisation, and Body Condition

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Abstract

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Spiders in agroecosystems play a role in natural pest suppression and contribute to biodiversity. In this thesis I have investigated if and when spiders recolonise cereal fields in spring when they have the potential to suppress establishing pest aphid populations. Furthermore, the influence of different environmental factors on spiders has been investigated to understand how it might be possible to provide suitable conditions for enhancement of their populations.

Linyphiid spiders recolonised fields after being negatively affected by sowing in spring, while lycosid spiders were unaffected. Conversely, lycosids showed a recolonisation in winter cereals after overwintering, but not linyphiids. But linyphiid migratory patterns also differed over time, because they were positively influenced by landscape heterogeneity in the beginning of spring but not at the end.

Diversity of lycosid and linyphiid spiders was positively influenced by perennial crops and forest in the surrounding landscape. Field margins were found to be a key habitat for the diversity of both spider families. Lycosid abundance was affected on the habitat scale and linyphiid abundance on the larger landscape scale, which can be explained by the families' different modes of dispersal. Farming systems, conventional or organic, contained different compositions of lycosid and linyphiid species. The dominant lycosid and linyphiid species were more abundant at organic sites.

Body condition of *Pardosa* (Lycosidae) turned out to be superior in landscapes dominated by large fields with annual crops, irrespective of farming system, perhaps because of less competition for available resources.

This thesis provides evidence that spiders are present in crop fields early in spring when they have the opportunity to suppress establishing aphid pests. Different spider species were associated with different farming systems, but the abundances of the most common species were enhanced by organic management. A diverse landscape with easy access to perennial crops and field margins will augment both number of species and individuals of spiders.

Keywords: Araneae, Lycosidae, Linyphiidae, landscape ecology, cereal crops, field margin, farming system, fecundity, pest management, generalist predators.

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Spindlar i odlingslandskapet

Mångfald, återkolonisering och kondition

Spindlar är betydelsefulla i odlingslandskapet därför att de som naturliga fiender har möjlighet att dämpa skadedjurspopulationer. På samma gång är spindlar både art- och talrika och berikar därför den biologiska mångfalden. I denna avhandling har jag undersökt om och när spindlar återkoloniserar stråsädfälten på våren när de potentiellt kan dämpa etablerande bladluspopulationer. Vidare har jag undersökt hur olika miljöfaktorer påverkar spindlar för att få kunskap om hur man bäst kan förse dem med så lämpliga miljöförhållanden som möjligt.

Efter vårsådden återkoloniserade spindelfamiljen Linyphiidae (mattvävarspindlar) fälten, men inte spindelfamiljen Lycosidae (vargspindlar). Det kan bero på att vargspindlarna inte blev påverkade av sådden, medan sådden gjorde att mattvävarspindlarna minskade i antal. Omvänt, i stråsäd sådd på hösten, återkoloniserade vargspindlar fälten på våren efter övervintringen, men inte mattvävarspindlar. Fast mattvävarspindlar visade också skillnad i spridningsmönster över tid då de var flera till antal i heterogena landskap under tidig, men inte sen, vår.

Mångfalden av vargspindlar och mattvävarspindlar påverkades positivt av mängden perenna grödor och skog i det omgivande landskapet. Fältkanter visade sig vara ett viktigt habitat för mångfalden av båda spindelfamiljerna. Antalet återfunna individer av vargspindlar påverkades på habitatnivå och inte på landskapsnivå, och tvärtom för mattvävarspindlar, vilket kan förklaras av deras olika spridningssätt. Vargspindlar sprider sig för det mesta på marken genom att springa eller gå, medan mattvävarspindlar ofta sprider sig via luften med hjälp av en silkestråd. Odlingssystem, konventionellt eller ekologiskt, innehöll olika sammansättningar av spindelarter. Dominerande arter återfanns till större antal i ekologiskt brukade fält.

Kondition hos *Pardosa*-spindlar (Lycosidae) visade sig vara bättre i landskap som bestod av stora fält med ettåriga grödor, oavsett odlingssystem. Kanske beror det på att det är lägre konkurrens om tillgängliga resurser i dessa landskap.

Med den här avhandlingen har jag visat att spindlar finns tillgängliga ute i fälten tidigt på våren när de har potentialen att hålla tillbaka etablerande bladluspopulationer. Olika arter av spindlar var förknippade till olika odlingssystem, men de vanligast förekommande arterna i odlingslandskapet förekom i högre antal i ekologiskt brukade fält. Ett omväxlande landskap med stor tillgänglighet till perenna habitat ökar både antalet arter och individer av spindlar.

Contents

Appendix

Papers I-V

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Öberg, S. & Ekbom, B. 2006. Recolonisation and distribution of spiders and carabids in cereal fields after spring sowing. *Annals of Applied Biology 149*, 203-211.

II. Öberg, S., Mayr, S. & Dauber, J. Landscape effects on recolonisation patterns of spiders in arable fields. (Submitted).

III. Öberg, S., Ekbom, B. & Bommarco, R. 2007. Influence of habitat type and surrounding landscape on spider diversity in Swedish agroecosystems. *Agriculture, Ecosystems and Environment.* In press.

IV. Öberg, S. Diversity of spiders after spring sowing – influence of farming system and habitat type. *Journal of Applied Entomology.* In press.

V. Öberg, S. Influence of landscape and farming system on body condition and fecundity of wolf spiders. (Manuscript).

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Introduction

Agriculture has been vastly intensified after the Second World War (Ihse, 1995; Krebs *et al.*, 1999). The agricultural landscape has changed drastically. Larger fields are planted with a limited selection of monoculture crops and use of pesticides and inorganic fertilisers have increased. These changes have resulted in several negative effects, such as species extinction, pesticide contamination and resistance, and nutrient leaching. Policies during the last decades have been working towards improving production methods in order to reduce these negative effects. One important aim has been to reduce insecticide use against pest insects. As an alternative to insecticides, farmers should, to a greater degree than previously, rely on pest suppression by natural enemies already present in the agroecosystem.

Predatory insects and spiders are believed to be important for the suppression of insect pest populations on arable land (Chiverton, 1987; Marc, Canard & Ysnel, 1999; Riechert, 1999). Generalist predators, such as spiders and carabid beetles, are thought to be more efficient than specialist predators for pest suppression in frequently disturbed habitats such as crop fields (Riechert & Lockley, 1984; Wiedenmann & Smith, 1997; Wissinger, 1997). Generalist predators can be sustained by alternative prey, for example detritivores, in the absence of herbivore prey (Chen & Wise, 1999). As a result, the predators can establish in the field at low pest densities. When aphids establish in cereal fields in late spring – early summer (Wiktelius, Weibull & Pettersson, 1990), a large part of the aphid population is active on or near the soil surface (Sopp, Sunderland & Coombes, 1987; Wiktelius, 1987). Thus, the ground living spiders and carabids can potentially find and feed on aphids during this period (the establishment phase). Early in spring the predators are unlikely to show prey preferences, instead they forage and catch whatever they encounter in order to survive (Harwood, Sunderland & Symondson, 2001). Moreover, studies in the laboratory and in caged plots have shown that spiders and carabids significantly suppress *Rhopalosiphum padi* (Linnaeus), the bird cherry-oat aphid, a common pest aphid in cereals (De Barro, 1992; Mansour & Heimbach, 1993; Kromp, 1999). Different kinds of gut content analyses (serological/PCR based) have also detected remains of *R. padi* in these predators, both in the aphid establishment phase and in the aphid exponential growth phase (Chiverton, 1987; A-K. Kuusk, personal communication). This demonstrates that spiders and carabids feed on aphids in the field. However, for the spiders to have a substantial effect on the aphids in cereal fields, they must be present in the field early in spring during establishment of the aphid population. It is at this time, before the aphid population grows exponentially, that spiders can have a substantial effect on the pest population (Fig.1). Even a moderate spider density might then create a favourable predator to pest ratio.

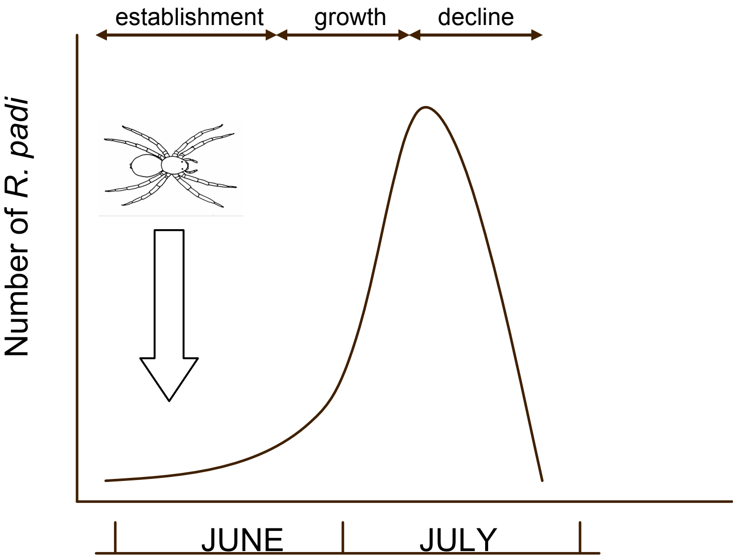

Fig. 1. Population development of the bird cherry-oat aphid in cereal fields. The arrow indicates when pest suppression by spiders and other generalist predators can be most effective; during the aphid establishment phase.

Dispersal data is essential when comparing predators' roles as pest suppressors (Coombes & Sotherton, 1986; Wissinger, 1997). It is important that the predators have a high dispersal ability to reduce the time lag between recolonisation of natural enemies and establishment of pest, which will lead to more successful pest suppression (Wissinger, 1997; Kromp, 1999; Marc, Canard & Ysnel, 1999). Annual crop systems are frequently disturbed, which can make it difficult for predators to remain in the fields. For example, cultivation methods, such as ploughing and harrowing, can cause predator mortality and emigration (Marc, Canard & Ysnel, 1999; Holland & Reynolds, 2003; Thorbek & Bilde, 2004). Therefore, for predators to occur in fields after such events, farmers are dependent on the predators' ability to recolonise. Immigration from other habitats in spring is necessary if predators are to be present in crop fields during pest establishment.

High abundance of spiders in perennial habitats during winter and spring suggests that these habitats are well suited for overwintering and an important source for immigration (Luczak, 1979; Marc, Canard & Ysnel, 1999; Pfiffner & Luka, 2000; Lemke & Poehling, 2002; Schmidt & Tscharntke, 2005a). 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). Structural simplification of landscapes, as in intensively managed regions, has been shown to reduce diversity and abundance of predators (Clough *et al.*, 2005; Schmidt *et al.*, 2005; Schmidt & Tscharntke, 2005b; Schweiger *et al.*, 2005; Bianchi, Booij & Tscharntke, 2006). Lower abundance in turn reduces the natural control potential of important crop pests (Riechert & Lawrence, 1997; Schmidt *et al.*, 2003). Östman, Ekbom & Bengtsson (2001) showed that a high perimeter to area ratio and high proportions of non-crop habitats in the surrounding landscape was positively related to the strength of predator impact on aphid establishment early in spring. Providing suitable environmental conditions for generalist predators promotes biocontrol of pests and can reduce costs in agriculture (Östman, Ekbom & Bengtsson, 2003).

Besides the spiders' role in pest suppression, they are also a substantial part of the total biodiversity in agroecosystems (Marc, Canard & Ysnel, 1999). But high predator diversity does not necessarily influence biological control (Bengtsson, 1998), and experiments testing the effects of species richness of natural enemies for biological control are contradictory (Finke & Denno, 2004; Snyder *et al.*, 2006). Straub & Snyder (2006) found that predator species identity was more important for effective pest suppression than increased species richness. Nevertheless, preserving biodiversity for spatiotemporal insurance for important ecosystem services such as biological control may be critical for coping with environmental changes in the future (Clergue *et al.*, 2005; Tscharntke *et al.*, 2005). Before drawing conclusions about whether or not high biodiversity is beneficial for biological control, we need information about the actual biodiversity in the ecosystem we are studying. There have been, up to now, no studies on spider diversity in major arable crops in Sweden, although studies have been carried out in several European countries. Again, generalist predators need to be enhanced by providing suitable settings for them, and therefore it is also necessary to study spider diversity in relation to different environmental conditions, such as landscape surroundings, habitat types, and farming systems.

The structure and composition of the surrounding landscape can influence spiders in crop fields, as mentioned before. In addition, the effect of the surrounding landscape on spiders may depend on the habitat type under study (Jeanneret *et al.*, 2003). Field margins are used by spiders as overwintering sites and refuges and can thus act as a source of dispersal to arable fields (Lemke & Poehling, 2002; Schmidt & Tscharntke, 2005a). An important question is whether many spider species prefer to stay in the surrounding habitats or if they actually move into the arable fields where they have the potential to suppress pests. The edge between the field margin and the arable field is noteworthy, because spider species that are normally only present in one of the two habitats (field margin and arable field) may meet in the overlapping edge (Samu, Sunderland & Szinetár, 1999). Suppression of insect pests by local populations of natural enemies is particularly important for farmers who wish to reduce or eliminate the use of agrochemicals. In organic management, where agrochemical applications are prohibited, the diversity of natural enemies may be economically important (Östman, Ekbom & Bengtsson, 2003). The effect of farming system on spider diversity is therefore essential to investigate in order to make best use of the potential of spiders as pest suppressors.

Several studies in other European countries have found that spider abundance is enhanced by organic management and in heterogeneous landscapes with high proportions of non-crops and/or perennial crops surrounding crop fields (Glück & Ingrisch, 1990; Pfiffner & Luka, 2003; Schmidt *et al.*, 2005; Schmidt & Tscharntke, 2005b; Thorbek & Topping, 2005). The question is: What are the mechanisms that promote enhanced spider populations in heterogeneous landscapes and organic management? As for spiders, carabid abundance and diversity have been shown to be enhanced by a complex landscape and organic management (Mäder *et al.*, 2002; Shah *et al.*, 2003; Bengtsson, Ahnström & Weibull, 2005; Purtauf, *et al.*, 2005). Body condition of carabids has been shown to be higher in organic than in conventional fields, and also enhanced by higher perimeter to area ratios of fields (e.g. smaller fields) in the surrounding landscape (Östman *et al.*, 2001). Also, for the carabid *Pterostichus cupreus* (Linnaeus), fecundity was lower in homogeneous landscapes with large field sizes, larger proportions of annual crops, and low perimeter to area ratios (Bommarco, 1988). Moreover, adult body size of *P. cupreus* was negatively related to average field size in the landscape. One explanation could be that the superior body condition and reproductive capacity of carabids may have caused the enhanced populations in these environments. To date there are no studies concerning body condition and fecundity of spiders in agricultural landscapes.

Study organisms

Spiders (Araneae) are predatory, carnivorous arthropods that feed on a variety of prey, which makes them generalists. Spiders mainly feed on insects and other arthropods, for example collembolans, dipterans, homopterans, and also other spiders. Different spiders apply different strategies in order to catch their prey. Some build webs, where the prey is caught. These spiders generally have long, thin legs that are suitable for constructing and living in a web. Other spiders catch prey by hunting, either by running and jumping on the prey or by letting the prey come to them. These spiders often have thick, stout legs, since they have better developed leg muscles than web spiders. Most spiders grow to maturity and mate in the course of a single year. Males die shortly after mating and females after laying eggs.

The spider families Lycosidae and Linyphiidae (Fig. 2) are common on arable land in Central and Northwestern Europe (Toft, 1989; Feber *et al.*, 1998; Samu & Szinetár, 2002; Pfiffner & Luka, 2003; Clough *et al.*, 2005) and they are known to have an impact on common insect pests such as aphids (Luczak, 1979; De Barro, 1992; Mansour & Heimbach, 1993; Lang, 2003). Lycosids are hunting spiders, mostly at ground level but occasionally in low vegetation. Besides catching prey when on the move, the lycosids also hunt using a "sit and wait" strategy and let the prey come to them. They react to vibrations, but also to visual cues. You can often see lycosids running around on warm, sunny days. Their hairy and brown appearance has given rise to the name wolf spiders. The lycosids perform brood care, both of the eggs and the newly hatched spiderlings. After laying eggs, the female carries the egg-filled cocoon attached to her spinnerets (Fig. 3). When the spiderlings hatch, she allows them to ride on her back for about a week for protection. Most lycosids species reproduce during spring – summer and overwinter as juveniles.

In contrast to lycosids, linyphiids catch prey in their sheet webs, which are most often situated at or near ground level. The spider runs upside down on the lower surface of its sheet web. The web is mended after a prey has been caught. Linyphiids are generally small with black or grey bodies, although they sometimes can have patterns and markings. Linyphiids either reproduce during winter (stenochronous) or from spring to autumn and overwinter in different stages (eurychronous). Linyphiids often disperse through the air attached to silk threads, which is called ballooning, and they can travel considerable distances. An important difference between the two families is their respective modes of dispersal (Luczak, 1979; Weyman, Sunderland & Jepson, 2002). Linyphiid spiders constitute a high proportion of aeronauts over agroecosystems, and lycosid spiders move mainly by walking. It was therefore relevant to separate these two families in the studies, in order to compare their responses to different factors in the environment.

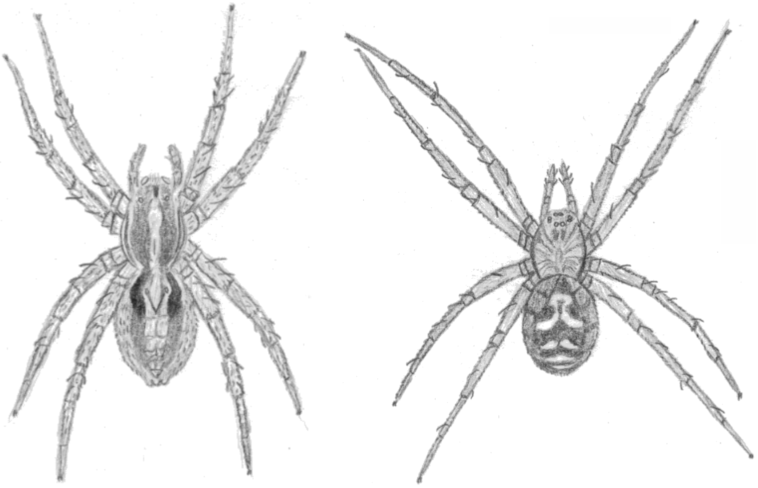

Fig. 2. Lycosid spider (to the left, natural size *ca.* 5 mm) and linyphiid spider (to the right, natural size *ca.* 2 mm). Note that other species belonging to the two spider families can have different appearances and sizes.

In *Paper I*, carabids (Coleoptera) were also included in the study on recolonisation of generalist predators after spring sowing. Carabids are common in agricultural landscapes and feed on pest aphids (Chiverton, 1987; Kromp, 1999).

Aims of the thesis

One of the underlying aims of this thesis was to explore if and when spiders recolonise cereal fields in spring in order to be present in the field before aphid establishment. In addition, to understand how the agricultural landscape should be structured to favour spiders, spider diversity in cereal fields and nearby habitats were investigated. I explored how spiders in these habitats are affected by different landscape surroundings and farming systems. The two common spider families Lycosidae and Linyphiidae have been compared because of their different characteristics. Finally, influence of landscape surroundings and farming system on body condition and fecundity of spiders has been studied as an additional aspect of suitable environments for spiders in the agricultural landscape.

I have specifically asked the following questions:

- Does sowing in spring have a negative impact on common generalist predators? (*Paper I*)
- Do common generalist predators recolonise cereal fields in early spring? (*Papers I,II*)
- Does the structure of the surrounding landscape influence spider recolonisation patterns in cereal fields? (*Paper II*)
- How is spider diversity influenced by habitat type, surrounding landscape, and farming system? (*Papers III,IV*)
- Do lycosid and linyphiid spiders respond differently to the factors included in the above questions? (*Papers I-IV*)
- Are body condition and fecundity of *Pardosa* spiders (Lycosidae) influenced by farming system and/or the surrounding landscape? (*Paper V*)

Materials and methods

Sampling

I have used pitfall traps to catch spiders in *Papers I-IV*. Reservations about pitfall traps have been raised in the literature, because they may not reflect the true abundance of arthropods, rather the activity density (Topping & Sunderland, 1992). Lycosid spiders are, however, most effectively collected with pitfall traps and it has been shown that the number of linyphiid species caught is about the same in pitfall traps as in D-vac trapping (Dinter, 1995; Standen, 2000). Also, one of the aims was to study the migration pattern of predators, and pitfall traps have been shown to be suitable for monitoring activity (Bishop & Riechert, 1990). Population densities of spiders are low in the vegetation zone of meadows and cereals and high on the ground (Nyffeler & Benz, 1987). Therefore, pitfall traps are a good choice for comparing spider catches among sites compared with alternative methods. All lycosids and linyphiids (*Papers I-IV*), and carabids (*Paper I*) captured in the pitfall traps were counted and adults identified to species.

In *Paper V*, where body condition and fecundity of *Pardosa* females were measured, females with eggsacs (Fig. 3) were caught by hand in the cereal fields. The female spiders were weighed and the cephalothorax widths were measured. The eggsacs were weighed and the number of eggs and/or juveniles in the eggsacs was counted.

Fig. 3. Pardosa female with eggsac.

Landscape parameters

In *Papers II, III* and *V*, the influence of the surrounding landscape on spider recolonisation, diversity, body condition and fecundity was assessed, respectively. Landscape parameters at each study site were calculated within a 500 m radius circle around the sampled field using geographical information system (GIS). It has been shown that 500 m is a suitable scale for studying spiders (Clough *et al.*, 2005; Schmidt & Tscharntke, 2005b).

In *Paper II*, study sites were situated in the agricultural landscape in the low mountain ranges of Central Hesse, Germany. Landscape parameters were based on a digital map of land use derived from aerial photographs from 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 boundaries between fields with different land use within a 500 m radius were calculated. 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 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. Therefore, only length of boundaries was used as a surrogate for the availability of refuge and hibernation sites for spiders in the surrounding landscapes.

In *Papers III* and *V*, study sites were situated in the vicinity of Uppsala, Sweden. Topographical GIS-data from the National Land Survey of Sweden were used, and also data on farmers' subsidies from the Swedish Board of Agriculture, where information on crops in each field are available. In each circle the proportion of the total area covered by: 1) forest, 2) non-crop areas other than forest (only *Paper III*), 3) perennial crops, and 4) annual crops were measured. Average size of arable fields and the number of fields in the surrounding landscape were also estimated, as measures of landscape heterogeneity. Note that the whole field did not have to be within 500 m to be included in the analysis.

Farming practices

In *Paper IV*, diversity of spiders in different farming systems, conventional or organic, was investigated. The main difference between conventional and organic fields was the use of herbicides and non-organic fertilisers in conventional management. Herbicides were used in all conventional fields. No fungicides were used except in one conventional field. No insecticides were used in the conventional fields during this year or the previous year. Conventional fields were fertilised with non-organic fertilisers, and organic fertilisers were used in all organic fields except two, which received no fertilisation at all.

In *Paper V*, body condition and fecundity of *Pardosa* spiders were studied in organic and conventional fields. As in *Paper IV*, the main difference between conventional and organic fields was the use of herbicides and non-organic fertilisers in conventional management. Herbicides were used in all conventional fields (except one), no fungicides were used (except on one conventional field), and no insecticides were used. Non-organic fertilisers were used in all conventional fields, and organic fertilisers were used in all organic fields except two (which were not fertilised at all). In order to see if there were any differences between the surrounding landscape of organic and conventional fields, a general linear model with farming system as a class variable was performed for landscape parameters. None of the landscape parameters differed between farming systems.

Statistical analyses

To study the recolonisation pattern of spiders (*Papers I,II*) and carabids (*Paper I*) the effect of time (*Papers I,II*) and distance into cereal the field (*Paper I*) on activity densities (*Papers I,II*) and species richness (*Paper II*) were analysed using a repeated measurement analysis of variance in procedure MIXED in SAS with compound symmetry as covariance structure based on Akaike information criterion (AIC). The difference in spider and carabid activity densities before and after sowing was tested in a paired, nonparametric Wilcoxon’s signed rank test (*Paper I*). The influence of surrounding boundaries on spider recolonisation was analysed using a linear regression for each of the three time steps (*Paper II*).

In the concept of diversity, not only species richness (number of species) is relevant. The abundance and composition of species also need to be studied in order to know which species that are present and how abundant they are in relation to other species. To study spider diversity in the agricultural landscape three different measures were used; species richness, activity density, and species composition (*Papers III,IV*). Both observed and rarefied numbers of lycosid and linyphiid species were analysed. A sample-based rarefaction was performed for each habitat (field margin, field edge, and field) at each site for Lycosidae and Linyphiidae using EstimateS 7.5 for Windows (Colwell, 2005). The x-axis from the rarefaction was re-scaled from number of samples to number of individuals. The number of species was then taken at the number of individuals from the habitat and site where the sampled number of individuals was lowest. Thus, the rarefied number of species for each site and habitat used in the analysis was corrected for number of individuals (Gotelli & Colwell, 2001). The activity density of Lycosidae and Linyphiidae, as well as the activity density of individual species that constituted >10% of the total number of adults of each family were analysed.

The effect of habitat type (field margin, field edge, and field) and landscape parameters were analysed separately in *Paper III*, because there were no interactions between habitat type and landscape parameters. The effect of habitat type on species richness and activity densities was tested in a two factor ANOVA, with habitat type as a fixed variable and site as random variable. The effect of landscape parameters and size of the sampled fields on species richness and activity densities was tested in a stepwise regression. In *Paper IV*, the effect of habitat type (field margin, field edge, and field) and farming system (organic or conventional) on species richness and activity densities was tested in a two factor ANOVA with habitat and farming system as class variables.

Species composition of Lycosidae and Linyphiidae was analysed using canonical correspondence analysis (CCA) (*Papers III,IV*). Forward manual selections with Monte Carlo permutations were done with landscape parameters, field size of the sampled field, and habitat types as environmental variables (*Paper III*), and with farming system and habitat types as environmental variables (*Paper IV*). The variables contributing significantly to the pattern of species composition were included in the final CCA. All multivariate statistics were done using Canoco 4.5 for Windows (ter Braak & Smilauer, 2002).

In *Paper V*, where body condition and fecundity of *Pardosa* spiders were studied in organic and conventional fields situated in differently structured landscapes, several landscape parameters correlated. All landscape parameters in the study were therefore combined into four principal components. Differences in body condition (residuals for relative female weight; Jakob, Marshall & Uetz, 1996) and fecundity measures (number of offspring and relative eggsac weight residuals) between farming systems and the four principal components were tested for in a general linear model with farming system as a class variable and principal components as continuous variables.

Statistical analyses were performed in SAS 8 and MINITAB 14 for Windows.

Results and Discussion

Recolonisation

Linyphiid spiders increased in numbers after being negatively affected by sowing in spring. They were also uniformly distributed in the field or showed a preference for the field after sowing. Lycosid spiders were not affected by sowing and were uniformly distributed in the cereal fields. This was also the case for the carabids. Thus, all these groups and species are potentially good pest suppressors (*Paper I*)

(Table 1). Lycosid spiders and carabids appeared to somehow avoid the negative effects of sowing better then linyphiid spiders. Thorbek & Bilde (2004) found that spiders were more sensitive to mechanical crop treatment than carabids. Many carabid species were significantly affected by ploughing in a study by Holland & Reynolds (2003), but this was apparently not the case when studying the effect of sowing. Results from studying the effect of soil cultivation on carabids are inconsistent in the literature (Holland & Luff, 2000), and it has been suggested that there is a need for detailed studies involving only one cultivation method at a time (Hance, 2002). Linyphiids, lycosids, and carabids were uniformly distributed from the edge and out into the field. Clough *et al.* (2005) found that most lycosids species were found in the edge, but accordingly, they also found that there was no difference in catches of the common lycosid species *Pardosa agrestis* (Westring) between the edge and the centre of the field. Also, the two common linyphiid species *Oedothorax apicatus* (Blackwall) and *Erigone atra* (Blackwall) did not show an edge preference which was the case in the present study as well (*Paper I*). The reasons for a uniform distribution may be a preference for environmental factors in the field, uniform distribution of necessary resources or interspecific competition (Luczak, 1979; Samu, Sunderland & Szinetár, 1999; Holland & Luff, 2000; Thomas, Holland & Brown, 2002). There were no interactions between trap distance into the field and sampling time, which means that it was not possible to detect a dispersal movement where predators first increased close to the edge and then later were found farther into the field. Many spiders, however, increased in activity density after sowing throughout the fields, which indicates a recolonisation.

Table 1. *Summary of recolonisation of spiders and carabids in spring and winter sown cereals. In spring sown cereals, the effect of sowing and distribution of generalist predators in the cereal fields was accounted for. In winter sown cereals, the landscape effect (total length of boundaries in the surrounding landscape) on recolonisation patterns was accounted for. Carabids were not included in the study in winter sown cereals*

	Spring sown cereals			**Winter sown cereals**	
Family	**Effect of sowing**	**Increase after sowing**	**Distribution after sowing**	**Increase after winter**	**Landscape effect**
Lycosidae	No	No	Uniform	Yes	No
Linyphiidae	Yes	Yes	Uniform	No	Yes (+), early in spring
Carabidae	No	No	Uniform	-----	-----

In contrast with the study on spider recolonisation in spring sown cereals (*Paper I*), lycosids increased over time during early spring in winter sown cereals fields, indicating a recolonisation, whereas linyphiids did not increase over time (*Paper II*) (Table 1). A reason for not detecting a recolonisation of the linyphiids in the study in winter sown cereals can be that they were present in the fields when the study started. The linyphiids 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 (Thomas & Jepson, 1997; Pfiffner & Luka, 2000; Lemke & Poehling, 2002). Possibly they had already migrated from overwintering habitats, thus making the recolonisation into fields faster than for lycosids. The reason why lycosids increased in the study in winter sown cereals and not in spring sown cereals can be because the study in winter sown cereals was conducted earlier in spring. Perhaps the lycosids recolonise early in spring, which was observed in the study in winter sown cereals but not in spring sown cereals. Lycosid species richness also increased over time in winter sown cereals, although maturation might have affected this result. In later spring, more spiders have probably moulted into adults, thus giving the pattern of increase in species richness, because only adult spiders were determined to species level.

The more cursorial lycosid spiders were clearly recolonising winter sown cereal fields, but this was not influenced by landscape heterogeneity. The species richness of the lycosids was, on the other hand, positively associated with boundaries in the surrounding landscape. Most likely fewer species arrived in crop fields in landscapes dominated by crops, because fewer species exist there. 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.

The linyphiids did not show an increase in activity density over time in winter sown cereals, but were positively affected by the total length of boundaries in the surrounding landscape (*Paper II*) (Table 1). For these spiders, however, there were also an influence of time, because the landscape effect was significant in the beginning but not at the end of the study. This might imply that landscape has an effect on early recolonisation of linyphiids, but not on the later migratory patterns. Schmidt & Tscharntke (2005b) 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 suggested that continued dispersal could have evened out the differences between landscapes later in the study or that linyphiids had approached maximum densities in the fields. These reasons can also explain the patterns of linyphiids in the current study.

Diversity of spiders

This is the first study of spider diversity in key and widely occurring agricultural habitats in Sweden (*Paper III*). Over the entire cropping season 18 lycosid species and 47 linyphiid species were collected. In Germany, UK, and Denmark; 13 lycosid species and 38 linyphiid species (Schmidt *et al.*, 2005), 14 lycosid species and 46 linyphiid species (Marshall, West & Kleijn, 2006), and 13 lycosid species and 58 linyphiid species (Toft, 1989) were found on arable land, respectively. The species compositions in these countries and in Sweden are similar. A recurring pattern is that for both families a few species dominate. In the current study, the lycosids *P. agrestis* and *P. palustris* (Linnaeus) and the linyphiids *O. apicatus*, *E. atra*, and *Meioneta rurestris* (C.L. Koch) were most abundant. These species are also dominant on arable land in several other European countries (Toft, 1989;

Feber *et al.*, 1998; Samu & Szinetár, 2002; Pfiffner & Luka, 2003; Clough *et al.*, 2005).

Over the whole cropping season, diversity of two spider families Lycosidae and Linyphiidae were both influenced by habitat type and the surrounding landscape but in different ways (*Paper III*) (Table 2). Species richness and composition of linyphiids were more sensitive to habitat type, whereas lycosid species richness and composition were influenced by the surrounding landscape. Thus, individual linyphiid species seemed to be more habitat specific than lycosid species. Linyphiid species richness (after rarefaction) was higher in the field margin and linyphiid species composition differed among habitat types. The observed number of linyphiid species was higher in the field than at the edge, whereas the field margin did not differ from either of these two habitat types. The difference between observed and rarefied number of linyphiid species among habitat types is almost certainly due to a more even species distribution in the field margin, and the occurrence of some dominant species in the field, which is in agreement with the results of linyphiid species composition. The higher number of rarefied linyphiid species in the field margin most likely resulted in a different composition of species there compared to in the cereal field and at the edge.

Species richness and species composition of Lycosidae were, in contrast with linyphiids, influenced by the surrounding landscape. Higher proportion of forest in the surrounding landscape was associated with higher numbers of observed lycosid species. Lycosid species composition was also influenced by the proportion of the landscape covered by forest. Schmidt *et al.* (2005) found that a high proportion of non-crop habitats increased local species richness, where forest constituted the largest part of the non-crop habitats under study. In this study, the proportion of non-crop areas other than forest was quite low. Thus, forest may constitute a source for spiders. In contrast to observed species richness, landscape did not have any affect on lycosid species richness after rarefaction in our study. Rarefied number of lycosid species was higher at the edge than in the field margin and in the field. In several cases the diversity measures differed between the edge and the other two habitats, which show the importance of including the edge between habitats when studying biodiversity. Interestingly, landscape surroundings had the same influence on spiders independent of habitat type.

For the activity densities, the pattern was the reverse of that for species richness and composition of the two families (*Paper III*). Lycosid activity density was affected by habitat type whereas activity density of linyphiids did not differ among habitats. The field margin, compared with the cereal field, contained a higher overall activity density of lycosids, which suggests a preference for the ley or grassland over the arable field, perhaps because of the less disturbed environment there, higher abundance and/or diversity of prey, and/or a more suitable microclimate. This corroborates previous findings where lycosids were more abundant in the field boundary (Clough *et al.*, 2005; Marshall, West & Kleijn, 2006). A study of lycosid assemblages across woodland-pasture boundaries also showed a change in the abundance of individual species rather than in species composition (Martin & Major, 2001). Linyphiid activity density was, in contrast, influenced by the surrounding landscape, which was not the case for the activity density of lycosids, and this is in accordance with the migration study in winter sown cereals (*Paper II*). The proportion of perennial crops in the surrounding landscape was central for the overall activity density of linyphiids. Several studies have showed that a high proportion of perennial crops and/or non-crops in the surrounding landscape have a positive effect on spiders on arable land (Halley, Thomas & Jepson, 1996; Clough *et al.*, 2005; Schmidt *et al.*, 2005; Schmidt & Tscharntke, 2005b; Thorbek & Topping, 2005; Bianchi, Booij & Tscharntke, 2006). Perennial habitats are generally disturbed less frequently, structurally and vegetationally more diverse than arable fields, suitable overwintering sites for spiders, and richer in prey abundance (Landis, Wratten & Gurr, 2000).

The spider families' different modes of dispersal may explain why the total activity density of lycosids is affected more by habitat type and linyphiids more by the larger scale landscape parameters. However, the activity density of one dominant lycosid species (*P. agrestis*) was unaffected by habitat type, and another dominant lycosid species (*P. palustris*) was positively influenced by the proportion of perennial crops in the surrounding landscape. Also, in contrast to the whole family, the two most dominant linyphiid species (*O. apicatus* and *M. rurestris*) had higher activity densities in the field edge and field than in the field margin, which strengthens the argument that these species are potential pest suppressors. The second and third most dominant linyphiid species (*M. rurestris* and *E. atra*) were not influenced by the surrounding landscape. These results indicate that common species do not necessarily show the same patterns as spiders at the family level.

The size of the sampled fields was included in the stepwise regression analysis as a covariate and turned out to affect spider diversity in several cases (*Paper III*). Both dominant lycosid species (*P. agrestis* and *P. palustris*) were negatively affected by large sizes of the sampled fields. In addition, size of the sampled fields and also average field size in the surrounding landscape affected lycosid species composition. It appeared that many of the common *Pardosa* species preferred the smaller fields that generally occur in a more heterogeneous landscape. A larger size of the sampled field had a positive effect on linyphiid activity density and also on the most abundant linyphiid species *O. apicatus*. It may be that there is no obstacle for linyphiid spiders to spread into the field, even for large fields. This can be explained by their mode of dispersal. An alternative explanation is intraguild interactions with *Pardosa* spiders that preferred smaller fields.

Table 2. *Difference among habitat types and landscape surroundings during a full cropping season (Paper III), and habitat types and farming systems during early spring (Paper IV) for activity density, species richness, and species composition of Lycosidae and Linyphiidae. --- = no effect. M = field margin, E = edge, F = field. For landscape parameters the sign in parentheses indicates the direction of the association. ORG = organic, CON = conventional. Environmental variables significantly affecting species compositions are shown*

	Full cropping season		**Early spring**	
Activity density	**Habitat type**	**Landscape parameters**	**Habitat type**	**Farming system**
Lycosidae	M > E > F	---	M > E = F	---
Linyphiidae	---	% perennial crops (+) Field size (+)	---	---
Species richness				
Observed Lycosidae	---	% forest (+)	M > E = F	---
Rarefied Lycosidae	M < E > F	---	---	---
Observed Linyphiidae	M ≥ E < F (F = M)	---	---	ORG < CON
Rarefied Linyphiidae	M > E = F	---	---	---
Species composition				
Lycosidae	---	% forest Average field size Field size	---	Significantly different ORG - CON
Linyphiidae	Field margin	---	Field	Significantly different ORG - CON

In *Paper IV*, diversity of lycosids and linyphiids were studied in different habitat types and farming systems during the critical period after sowing before aphid establishment in cereal fields (Table 2). As in *Paper III*, where spider diversity during a full cropping season was studied, habitat type influenced the two spider families in different ways. Once more, linyphiid species composition was affected and lycosid composition unaffected by habitat type. However, linyphiid species composition was significantly influenced by the field margin over the whole cropping season and by the crop field in spring. In contrast with *Paper III*, there was no difference in number of linyphiid species between habitat types, indicating that the field contained different species and that some species had higher activity densities there than in the other habitat types. Thus, these species had migrated into the fields early in the cropping period. Activity density of lycosids, as well as lycosid species richness, was higher in the field margin, whereas the activity density of linyphiids did not differ among habitat types. Again, the underlying reason may be that the more far-reaching dispersal of linyphiids renders them less dependent on habitat type than lycosids.

Farming system, conventional or organic, had a number of effects on lycosid and linyphiid diversity. The species compositions of both spider families, Lycosidae and Linyphiidae, were different when comparing the two farming systems. Observed species richness of linyphiids was higher at conventional sites, which was not the case for lycosid species richness. The different composition of Linyphiidae between farming systems is most likely due to the fact that some species occurred only at conventional sites, although some linyphiid species were more common at organic sites. The higher number of linyphiid species at conventional sites might be because of less competition from common linyphiid and lycosid species that were more abundant at organic sites. Feber *et al.* (1998) showed a higher species richness of spiders in fields with organic management, although organic and conventional fields had different compositions of spiders and five linyphiid species were found only at conventional sites. Schmidt *et al.* (2005) did not find a significant difference in spider species richness between organic and conventional fields, although they found more linyphiid species in conventional fields (34) than in organic (26), which is similar to the findings in the current study (Con: 33; Org: 24). The lycosid species richness did not differ between farming systems, and almost all lycosid species were found at both organic and conventional sites. This suggests that the difference in species composition between farming systems is due to relatively different numbers of caught individuals of each species. Many *Pardosa*-species seemed to be more common at organic sites. Furthermore, the activity density of dominant lycosid (*P. agrestis*) and linyphiid (*O. apicatus*) species was significantly higher at organic sites. These two dominant species have been shown to be more common in organic fields in other studies as well (Pfiffner & Luka, 2003; Schmidt *et al.*, 2005). The reason why *P. agrestis* and *O. apicatus* do better at organic sites can be due to lack of use of herbicides, which can create a higher diversity of prey caused by a more diverse vegetation structure (Feber *et al.*, 1998; Samu, Sunderland & Szinetár, 1999; Sunderland & Samu, 2000). In addition, organic fields are often fertilised with manure. This organic practice may add diversity to the soil structure and increase the abundance of prey and in turn the abundance of spiders (Samu, Sunderland & Szinetár, 1999).

Body condition and fecundity of *Pardosa* spiders

Landscapes containing large fields with annual crops and low amounts of forest had a positive influence on the body condition of *Pardosa* females (*Paper V*) (Fig. 4). Fecundity was not associated with landscape features and there was no difference in body condition and fecundity between farming systems. In contrast, fitness-related traits of carabids have shown to be positively influenced by organic management, low proportions of annual crops, and small field sizes in the surrounding landscape (Bommarco, 1998; Östman *et al.*, 2001). As mentioned, organic management and heterogeneous landscapes have been shown to enhance spider populations, as well as carabid populations. In addition, *Paper III* and *IV* showed that common *Pardosa*-species had higher activity densities in landscapes with smaller fields and higher proportions of perennial crops, and in organic fields in the same study region as in *Paper V*. If available food is the main limiting factor on the number of spiders, then fitness-related traits, such as body condition and fecundity, may be constant as a result of increased level of competition for resources at high population densities, even though resources are plentiful. Spider competition can potentially occur in agroecosystems (Marshall & Rypstra, 1999) and spiders can numerically respond to available food (Wise, 1993). This might have been the case in the different farming systems, where body condition and fecundity turned out to be the same. Thorbek, Sunderland & Topping (2004) found only minor differences in the fecundity of linyphiid spiders between agricultural habitats, and suggest that it can be due to higher levels of competition in the richer grassland habitats than in the spring cereal field. On the other hand, if the limiting factor for spiders to reach high densities is something other than available food, for example lack of overwintering sites, then spiders might have access to relatively more food resources. This could explain the superior body condition of spiders in homogeneous landscapes when compared to heterogeneous landscapes. In landscapes dominated by large, annual crop fields, spiders have less access to perennial habitats, which are important refuges for spiders during winter (Pfiffner & Luka, 2000; Schmidt & Tscharntke, 2005a). As fecundity was not influenced by the surrounding landscape, this suggests that excessive resources were allocated to body condition rather than reproductive capacity in the *Pardosa* females. A better body condition may be advantageous for better brood care, or maybe facilitates the building of another eggsac later in the season.

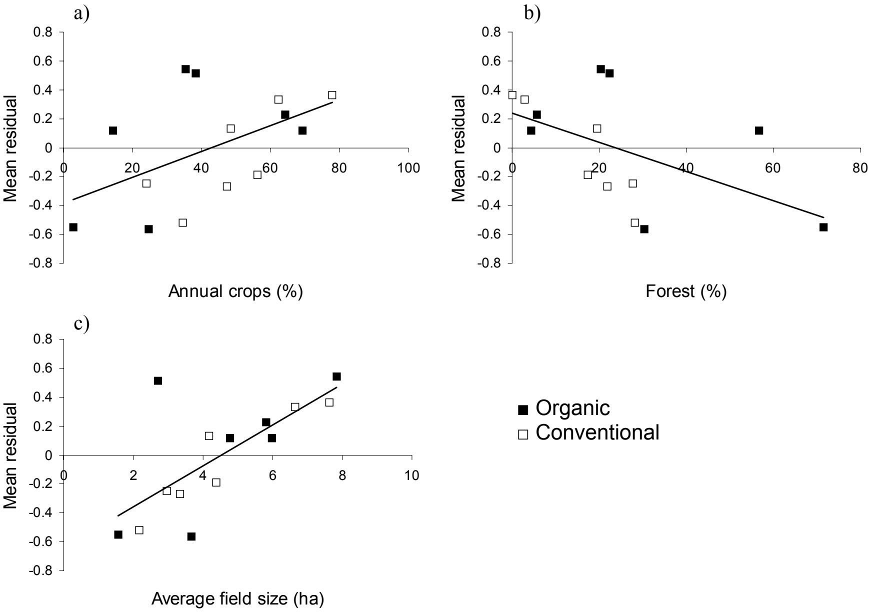

Fig. 4. Body condition (relative female weight residuals) of *Pardosa* females against a) percentage of annual crops, b) percentage of forest, and c) average field size in the landscape. There was no difference in body condition between organic and conventional fields.

Conclusions and future challenges

One long term goal, leading to improved agricultural management and avoiding negative aspects of intensification, is to rely on natural enemies for biological control of pests instead of using chemical inputs. The present thesis aimed to resolve various issues to facilitate reaching this major goal. One objective was to study the recolonisation of spiders and other generalist predators to cereal fields at the critical time in spring when their potential to suppress establishing pest aphid populations is highest. Furthermore, spider populations in the agricultural landscape may need to be abundant and diverse if pest populations are to be held below damage thresholds. For that reason, the influence of different environmental factors on recolonisation, diversity, and fitness-related traits of spiders have been investigated to understand how to provide suitable conditions for them.

This thesis shows the importance of including generalist predators' timing of dispersal on arable land when studying their potential role as biological control agents. Disturbed crop fields must be recolonised by predators. Here one such disturbance, sowing, was studied. Sowing is not only close in time to the colonisation of the field by pest aphids, but also an unavoidable crop husbandry practice. In this study, predators that were negatively affected by the disturbance of sowing increased in the fields early in the cropping season. In addition, many of the predators that were not affected by sowing were uniformly distributed in the fields. Several studies conducted in late spring or early summer have shown that a diverse landscape increases spider abundance and diversity in crops. Here, it has been shown that the recolonisation of spiders to cereal fields during early spring appears to be positively influenced by the enrichment of non-crop habitats in the surrounding landscape. Altogether, this means that certain predators have a good opportunity to encounter and feed on the establishing aphids, and thereby can contribute to preventing a pest outbreak.

A high coverage of perennial crops and forest together with neighbouring habitats, such as field margins, will augment the number of species and individuals of spiders in the agricultural landscape. This is clearly demonstrated for Swedish agroecosystems in this study. These environmental variables have been demonstrated to enhance populations of generalist predators in numerous studies in several European countries, and I suggest that, from now on, these facts ought to be viewed as common knowledge. In order to support pest suppression by generalist predators, significant proportions of perennial habitats should be provided in the agricultural landscape.

Pardosa-spiders (Lycosidae) are common in agroecosystems and were found to be enhanced in heterogeneous landscapes with high proportions of perennial crops and also by organic management. On the other hand, *Pardosa*-spiders had superior body condition in landscapes with large, annual crop fields irrespective of farming system. It is suggested that spiders have better body condition in homogeneous landscapes due to less competition for available resources. To explore this proposal, further studies are needed to investigate at which densities (levels of competition) body condition of spiders is affected in environments with different amounts of available resources. Temporal environmental variation over large areas has been found to be more important for the condition of carabids than spatial environmental variation (Östman, 2005). Temporal variation during the year and between years in spiders' body condition in different environments also needs supplementary consideration before drawing final conclusions on how body condition of spiders affects populations in the agricultural landscape.

Many lycosid spiders were found to a larger extent in field margins than in crop fields and this is a potential problem for biological control. If the number of predators is too low in the crop for sufficient pest suppression, we need to attract spiders from the field margin into the field. How high predator densities need to be for suppression of pests in the field, and how to attract spiders into crop fields are challenging questions that need more attention. The field margin should be a source of potential pest suppressors, not a favoured habitat that holds them there.

Occasionally, different spider species were associated with different environments and farming systems. Some were more commonly caught in heterogeneous landscapes with small field sizes and other species in larger field sizes. For the different farming systems, the commonly caught species were generally found in high numbers at organic sites and rarely caught species at conventional sites. It is difficult to know which factors influence these different outcomes and how to choose which environmental variables to modify in order to obtain enhanced predator populations, especially when different spiders are affected in different ways. If the reason for enhancing spider populations in crop fields is to improve biological control, we need to investigate if a high number of spider species facilitates biocontrol, or if high abundance of certain key species is the most important factor. Together with studies on diversity in different environments, such as in the present thesis, experimental studies on functional diversity will provide additional information on how agroecosystems should be structured in order to enhance the species that have the most potential as natural enemies of common pests. Overall, this thesis is based on observational studies, and future challenges will be to investigate and explain the mechanisms behind the observed patterns before we can realise the goal of sufficient pest suppression by natural enemies in the agricultural landscape.

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‘*If there is a large gathering of spiders, everything will be satisfactory*’
(2000 years old Chinese writing).