Local and landscape management effects on syrphid fly guilds: flower strips, farming practice and hedges

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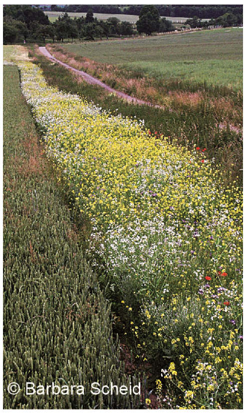
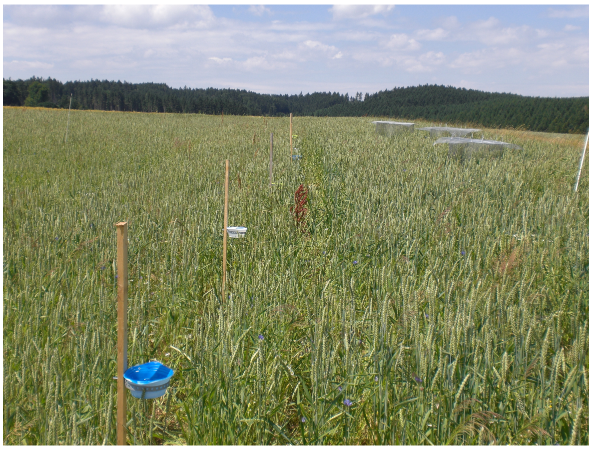
CHAPTER 1

General introduction





Introduction

During the last decades, agriculture has transformed into highly productive economical systems in order to answer globally increased demands for agricultural products (Robinson & Sutherland 2002; Tilman *et al.* 2002). Conversion of uncultivated (semi-natural and natural) habitats and intensified land use practices, however, resulted in a dramatic decrease of biodiversity in agricultural landscapes during the last decades (Benton *et al.* 2003; Weibull *et al.* 2003). Modern agricultural landscapes are often characterized by low structural complexity and habitat connectivity, thereby negatively affecting species movements within the agricultural matrix. Such processes have been shown to increase local species extinction (Harrison 1991; Fahrig 2003), affect genetic exchange (Templeton *et al.* 1990; Schmitt & Seitz 2002), thereby threatening farmland species and maintenance of related ecosystem services such as biological control and pollination (Cunningham 2000; Tscharntke *et al.* 2005).

Semi-natural habitats in agricultural landscapes are important for the maintenance of farmland biodiversity, providing hibernating and reproduction sites, food resources and shelter from disturbances. On the other hand, annual crops only form temporal habitats and resources due to annual harvesting and crop rotation (Geiger *et al.* 2009). Classical habitat-management schemes in order to mitigate the negative effects of agricultural intensification (Altieri & Farrell 1995; Wratten & van Emden 1995; Östman *et al.* 2001) often focus on local scales only (Landis *et al.* 2000). For example, the introduction of semi-natural grassy field margins and flower strips, and also low intensity farming practices such as organic farming, have been shown to enhance ground-dwelling and flying predators as well as parasitoids, thereby positively influencing biological control of agricultural pests (Salveter & Nentwig 1993; Frank 1999). However, there is an increasing body of literature showing that also landscape context is an important factor determining species distributions and occurrences (Haynes *et al.* 2007; Farwig *et al.* 2009; Batáry *et al.* 2011). For example, in structurally simple landscapes, organic farming practices have been shown to be most effective, while in structurally complex landscapes positive effects of organic farming on biodiversity can be superimposed, because of a generally higher biodiversity (Tscharntke *et al.* 2005). Thereby the landscape matrix filters for specific species traits such as dispersal abilities, degree of specialization, and/or trophic position (Purtauf *et al.* 2005; Schmidt *et al.* 2008). Also the spatial scale at which environmental changes occur can have profound effects on the distribution and abundance of particular species in agricultural matrices (Holland *et al.* 2004). For example, solitary wild bee species respond to high heterogeneity of habitats at relatively small spatial scales (~1km) (Steffan-Dewenter *et al*. 2002), whereas bumblebees (with bigger foraging ranges) respond to habitat heterogeneity at larger spatial scales (up to 3 km) (Westphal *et al*. 2006). Therefore, environmental schemes and measurements should be advised to consider habitat management at local and landscape scales simultaneously (Tscharntke *et al*. 2007).

Study area and organisms

The studies conducted for this thesis were carried out in arable landscapes of Germany and Sweden, using study areas dominated by arable crops such as winter wheat, summer barley and oilseed rape, interspersed with semi-natural habitats such as forests, hedgerows, grassland and fallows. The amount of arable fields in relation to semi-natural areas greatly differed among study sites (Fig. 1; Study in Chapter 2 and study 2 in Chapter 3).

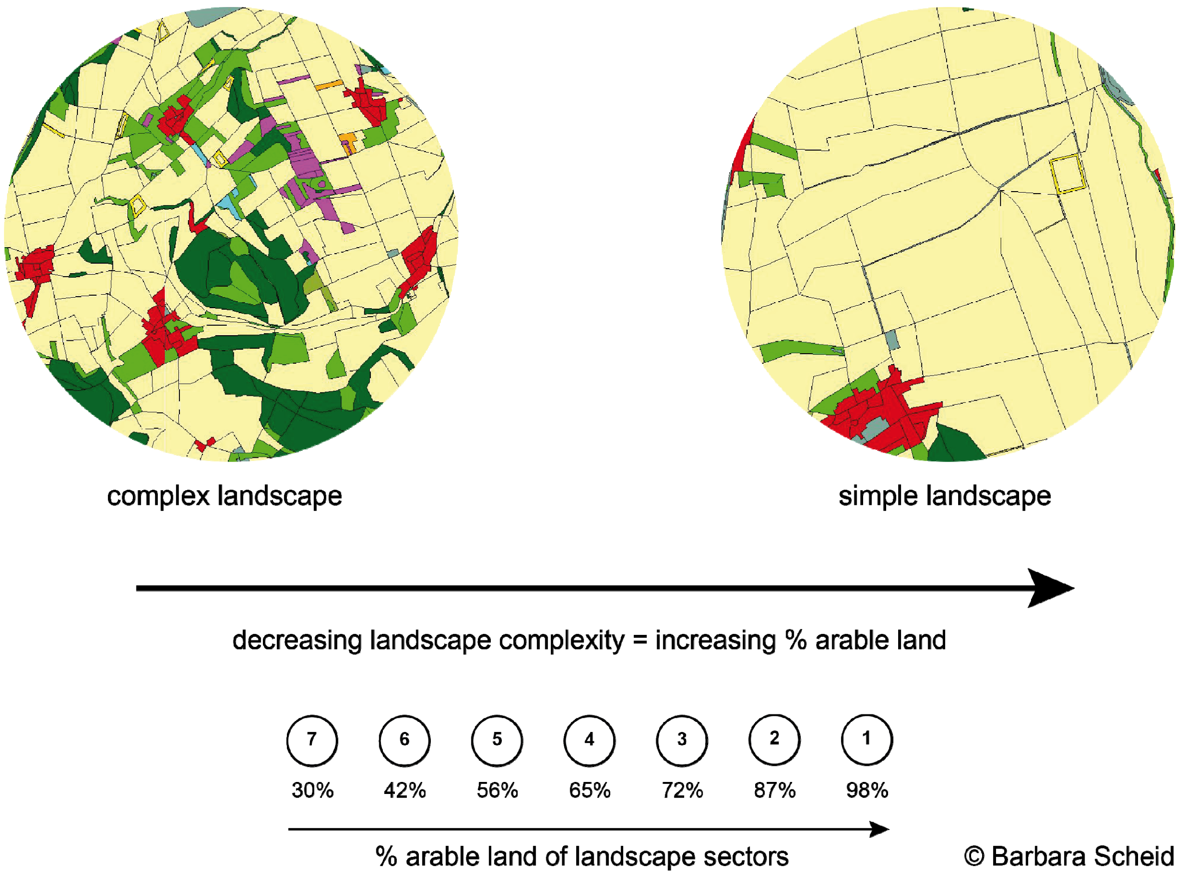


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Fig. 1: Schematic drawing of the study design (Chapter 2): we selected 7 landscape sectors of a 1000 m-radius along a gradient of varying landscape complexity, which is associated with the percentage of arable land, showing the two extremes of complex and simple landscapes.

The proportion of arable land has been shown to be a simple predictor of landscape complexity because of its close correlation to other landscape parameters such as habitat type diversity and habitat isolation (Thies & Tscharntke 1999). In study 3 (Chapter 4) we additionally investigated the influence of varying oilseed rape proportions in landscapes sectors of 1 km radii around study sites.

In all studies, we focused on syrphid flies (Diptera: Syrphidae), which include species that are important predators and pollinators in agricultural landscapes. Syrphid flies are one of the biggest groups of Diptera with over 90 genera and more than 800 species occurring in Europe (Oosterbroek 2006). Adult syrphid flies are pollen and nectar feeders, while syrphid larvae show a wide spectrum of feeding types such as mycophagous, phytophagous, zoophagous or saprophagous. In agricultural landscapes, aphidophagous syrphid species such as *Episyrphus balteatus*, *Sphaerophoria scripta*, *Melanostoma scalare* can play an important role for biological control of cereal aphid pests (Chambers 1986; Chambers & Adams 1986). Moreover, syrphid flies are known to be effective pollinators of crop plants (e.g. *Brassica napus* L.) (Jauker & Wolters 2008). Many other arthropods contribute to the functioning of ecosystem services. For example, lacewings (Chrysopidae), lady beetles (Coccinilidae), spiders (Araneae) or parasitoid wasps (Hymenoptera) are predators of cereal aphids, which can add to the overall pest control potential (Sundby 1966; Schmidt *et al.* 2003; Mills 2005). However, the relative importance of certain natural enemy groups for biological control is not studied well. Recent studies with selective exclusion experiments of natural enemies support the idea that flying predators (and parasitoids) might be most effective biocontrol agents (Holland *et al.* 2008; Thies *et al.* 2011).

Chapter outline and hypotheses

In the studies presented in this thesis, the importance of local habitat measurements on syrphid fly species richness and abundance was investigated by comparing four types of ecotone habitats (narrow and broad sown flower strips, naturally developed grassy strips and the boundary of adjoining wheat fields as control) along a gradient of landscape complexity, ranging from 30-100 % of arable land in the surroundings of the study sites (Chapter 2). The influence of farming practices (low vs. high levels of agricultural intensification in cereal fields) was investigated across two European regions (Germany versus Sweden) to enlighten region-specific differences in population development and diversity (Chapter 3). In the third study (Chapter 4), syrphid fly abundances in three types of semi-natural landscape elements (forest margins, forest-connected and isolated hedgerows) were analysed with respect to the influence of varying proportions of mass-flowering oilseed rape at the landscape scale (oilseed rape and wheat fields) and the local cropping systems (winter wheat and oilseed rape).

The following hypotheses were tested:

(i) Species richness and abundance of syrphid flies are increased in sown flower strips compared with naturally developed field margins and wheat fields (Chapter 2).

(ii) The effect of sown flower strips on syrphid species richness and abundance is more pronounced in structurally simple landscapes compared with complex landscapes (Chapter 2).

(iii) Species richness and abundance of syrphid flies are higher and peak earlier in the season in the southern region (Germany) compared to the northern region (Sweden) owing to favourable climatic conditions (Chapter 3).

(iv) Aphidophagous syrphid flies are more abundant in landscapes with high levels of agricultural intensification due to higher larval food availability (Chapter 3).

(v) Non-aphidophagous syrphid flies benefit from landscapes with low levels of agricultural intensification owing to food resources outside crop fields (Chapter 3).

(vi) Abundances of syrphid flies differ among semi-natural habitats differing in the degree of exposure to adjacent crops (forest edges, forest-connected hedges and isolated hedges) and these differences among semi-natural habitats affect syrphid fly spillover between the semi-natural habitats and the adjacent crop fields (Chapter 4).

(vii) Abundances of syrphid flies in semi-natural habitats are higher adjacent to oilseed rape than adjacent to wheat, because of higher local spillover from mass-flowering oilseed rape (Chapter 4).

(viii) Spillover is more pronounced in landscapes with low than high percentages of oilseed rape, because of landscape-scale dilution of syrphid flies in landscapes with high percentages of oilseed rape (see Fig. 1 in Chapter 4).

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CHAPTER 2

Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes

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Abstract

1. The structural complexity of agricultural landscapes influences the local biodiversity and associated ecosystem services. Hence, developing effective biodiversity management requires a better understanding of the relative importance of local and landscape changes, especially for functionally important organisms such as hoverflies benefiting from flowering plants.

2. We examined hoverfly (Diptera: Syrphidae) communities in broad and narrow sown flower strips, in naturally developed grassy strips and in wheat fields (as a control). We also investigated the effects of these four habitat types on syrphid occurrence in the adjacent wheat fields.

3. The relative influence of local vs. landscape effects was tested by selecting study sites along a gradient of structural complexity from simple landscapes (~100 % arable land) to complex landscapes (up to 70% semi-natural habitats such as fallows, field margins, hedges and grassland). Landscape complexity was assessed within landscape sectors of 0·5–4·0 km radius around strips.

4. Syrphid density and in particular, the density of aphidophagous species, was higher in narrow and broad sown flower strips compared to grassy strips and wheat–wheat boundary controls at the milk-ripening stage of the wheat. In addition, species richness of aphidophagous syrphids within wheat fields adjacent to broad sown flower strips was higher at the wheat peak-ripening stage. This indicates a spillover between habitats and a positive effect of these sown flower strips on potential biocontrol of cereal aphids. Flower densities and syrphid diversity and density, respectively, were closely related.

5. Species richness and abundance in the sown flower strips increased as the proportion of arable land in the surrounding landscape increased, suggesting that within structurally simple landscapes (at 0·5–1 km radius around the sites) syrphid flies concentrated on the most rewarding resources within the sown flower strips. Sown flower strips were more effective at increasing syrphid species richness and abundance in simple landscapes, presumably because the creation of flower resources made the greatest difference in such homogeneous, intensively managed arable landscapes.

6. *Synthesis and applications*. Agri-environment schemes should take the surrounding landscape characteristics into account when considering using sown flower strips to enhance syrphid density and diversity, and their biocontrol function, in arable landscapes. Creating locally such flower strips is more effective in simple landscapes containing a high proportion of arable land, while in complex landscapes, keeping the overall diversity is important.

Key-words: *agricultural intensification, biocontrol, concentration effects, flower strips, landscape complexity, semi-natural habitats, syrphids*

Introduction

The loss and fragmentation of semi-natural habitats in modern agricultural landscapes leads to a reduction in species richness and abundance. This decrease in biodiversity may affect important ecosystem services such as biological control (Saunders, Hobbs & Margules 1991; Tews *et al*. 2004). Habitat management that changes agricultural practices within crop fields, or the management of agricultural landscapes, such as natural habitat conservation, have been shown to mitigate the effects of agricultural intensification (Altieri 1995; Burel & Baudry 1995; van Driesche & Bellows 1996; Matson *et al*. 1997; Menalled *et al*. 1999; Thies & Tscharntke 1999; Tscharntke & Kruess 1999; Tscharntke 2000; Halaj & Wise 2001; Östman, Ekbom & Bengtsson 2001; van Nouhuys & Hanski 2002; Tscharntke et al. 2002; Wratten & van Emden 1995).

Field margins of various forms are found adjacent to arable fields (Marshall 1988). In landscapes dominated by agriculture such ecotones may represent most semi-natural habitats (Bazin & Schmutz 1994; Burel & Baudry 1999). At the local scale, the introduction of sown flower strips and weed strips increases habitat diversity and numbers of both ground-dwelling and flying predators and parasitoids, thereby improving biological pest control (Lys & Nentwig 1992; Salveter & Nentwig 1993; Frank 1999; Thies & Tscharntke 1999). Improving habitat diversity at the landscape scale also enhances local biodiversity and such ‘matrix effects’ may be important for many groups of beneficial arthropods (Burel *et al*. 1998; Weibull, Bengtsson & Nohlgren 2000; Atauri & de Lucio 2001; Jeanneret, Schüpbach & Luka 2003; Clough *et al*. 2005; Schmidt *et al*. 2005; Schweiger *et al*. 2005; Thies, Roschewitz & Tscharntke 2005; Tscharntke *et al*. 2005). However, different species ⁄groups respond to landscape complexity at different spatial scales. For example, arable spider species show contrasting responses to landscape-scale modification with respect both to the direction and the spatial scale of the relationship (Schmidt *et al*. 2008). The species richness of carabid beetles was shown to increase with percentage cover of grassland in the surrounding landscape, and activity density followed the same trend (Purtauf *et al*. 2005). Undisturbed perennial habitats appeared to enhance both cereal aphid pests and aphid parasitoids (Thies *et al*. 2005).

Hence, the landscape matrix appears to be related to local patterns of diversity, selecting for species traits such as dispersal ability (Tscharntke & Brandl 2004). The relative importance of natural enemy groups in the biological control of cereal aphids is little understood, but flying predators and parasitoids have been shown to be most effective in selective exclusion experiments (Schmidt *et al*. 2003; Holland *et al*. 2008). However, the relative abundance of naturally occurring enemy species differs greatly among years and regions (Krause & Poehling 1996; Östman *et al*. 2001; Schmidt *et al*. 2003; Thies *et al*. 2005). Syrphid flies (Diptera Syrphidae) are a species-rich group involving over 500 phytophagous, saprophagous and zoophagous species in Europe (van Veen 2004). The natural habitats of these functional groups are related to the availability of larval food resources. Aphidophagous species, which represent the dominant group, use a wide range of habitat types including arable fields harbouring aphid pests, whereas phytophagous and saprophagous species predominantly are restricted to non-crop habitats because of their specific food resource requirements (Raskin, Glück & Pflug 1992; Frank 1999). The adults of all functional syrphid groups feed on pollen and nectar of flowering plants. Therefore, they are expected to benefit from flowering plants, e.g. flower rich field margins (Chambers & Aikman 1988; Cowgill, Sotherton & Wratten 1992; Hickman & Wratten 1996). The role of aphidophagous syrphid species in suppressing cereal aphid outbreaks and methods of increasing the population size through local and landscape diversification has been reported in previous studies (Chambers & Adams 1986; Chambers *et al*. 1986; Tenhumberg & Poehling 1995; Schmidt *et al*. 2003; Brewer & Elliott 2004). However, the influence of, and the interaction between, local and landscape scale diversity on syrphid populations is little known, because most studies have been conducted at one scale only.

In this study, we analysed the relative importance of local and landscape structural diversity on syrphid fly species richness and abundance by comparing four types of ecotone habitats adjacent to winter wheat fields occurring across a gradient of landscape complexity (~ 30–100% arable land): broad sown flower strips (BFS), narrow sown flower strips (NFS), naturally developed grassy strips (GS) and the boundary of adjoining wheat fields lacking such strips (as a control). Syrphids are an interesting group for the study of effects of agricultural intensification as they are very mobile compared with many other insect groups; and therefore, may contribute to the preservation of ecosystem services such as biocontrol and pollination in intensified agricultural landscapes (Jauker *et al*. 2009). We expected that (i) species richness and abundance of syrphids would be increased in flower strips compared with naturally developed field margins and wheat fields and that (ii) this effect would be more pronounced in structurally simple landscapes compared with complex landscapes (hypothesized by Tscharntke *et al*. 2005).

Materials and methods

Study area and study design

The study was conducted in the vicinity of the city of Göttingen (51°54′ N, 9°93′ E), Lower Saxony (North Germany). The area is under intensive agricultural use (c. 75%) dominated by arable fields and interspersed with fragments of semi-natural habitats such as forests, hedges and grasslands (Steffan-Dewenter *et al*. 2002). The average temperature and total rainfall during the study period in June and July 2006 was 17·9 °C and 0 mm (20–23 June); 20·9 °C and 44·6 mm (11–14 July) and 22·3 °C and 11·1 mm (27–28 July); data from the Meteorological Station, Göttingen.

We analysed syrphid species richness and abundance in five types of habitats: GS (c. 3m wide, n = 7); NFS (c. 3-6 m wide, n = 7); BFS (c. 12-25 m wide, n = 7); the boundary of adjoining wheat fields lacking such strips (as a control and which we refer to as wheat–wheat boundary, n = 7); and within the wheat fields adjacent to each of the preceding habitats (n = 4·7 = 28). Agri-environmental schemes in Lower Saxony include incentives for the creation of NFS and BFS in the agricultural landscapes. For this study, we selected strips adjacent to wheat fields that were located along a gradient of surrounding landscape complexity, ranging from ca. 30% to 100 % arable land, with a mean distance of 18·3 km between study fields. We measured the proportion of arable land in circular sectors at four spatial scales (radii of 0·5, 1, 2 and 4 km) around each study site using official digital thematic maps (ATKIS-Digitales Landschaftsmodell 25 / 1; Landschaftsvermessung und Geobasisinformation, Hannover, Germany 1991–1996) and the Geographical Information System ArcView 3.1 (ESRI Geoinformatik GmbH, Hannover, Germany). The proportion of arable land has been shown to be a simple predictor of landscape complexity in our study area because of its close correlation with other landscape metrics such as habitat type diversity and habitat isolation (Thies & Tscharntke 1999; Steffan-Dewenter *et al*. 2002).

Sampling of syrphid flies

Syrphids were captured along 100 m transects by sweep netting (c. one sweep per footstep) (i) within the strip habitats and (ii) within the adjacent winter wheat field along a transect parallel to the strips (6 m distance to strips) and at a distance of 6 m from the edge of the strip habitat. The wheat–wheat controls were sampled in a similar way along transects running directly along the boundary between the two fields (within 3 m of the boundary at both sides). Sampling was carried out at three consecutive periods: (i) at wheat flowering stage (20–23 June); (ii) at wheat milk ripening stage (11–14 July); and (iii) at winter wheat peak-ripening stage (27–28 July). All invertebrates collected were placed in 3-L plastic bags, cooled, and then taken to the laboratory. The syrphid species were separated from all other arthropod genera and identified, where possible, to species level using identification keys (van Veen 2004). Species were sorted into two trophic groups according to their larval feeding type: aphidophagous feeding type and saprophagous, detrivourous and bacteria eating feeding type (a list of species is available in Appendix S1, Supporting Information).

Flower densities in ecotones

Flower density in each of the 28 habitats was measured, at the same time as syrphids were sampled using a standardized estimation procedure for each strip. Flowers within the conventional managed wheat fields were almost absent, so flower density was around zero. A ring with an area of c. 0·75 m2 was placed on the ground 10 times per strip at 10-m intervals per habitat at the same locations used for the syrphid samplings. The number of flowers of all flowering plants was counted and the flower density was calculated for an area of 1 m^2. Plants were identified up to species level using Rothmaler (1994) (a list of plant species is available in Appendix S2, Supporting Information).

Statistical analyses

We analysed syrphid species richness and abundance (per 100m transect) using general linear models (GLM) to test the influence of (i) habitat type (NFS, BFS, GS and control fields) nested in site; (ii) site (wheat field vs. adjacent habitat); and (iii) landscape complexity (the proportion of arable land at four spatial scales, 0·5–4 km radius of landscape sector). Model assumptions were tested by examining the Gaussian distribution of the residuals. All non-significant main effects and interactions were removed from the models by using a backwards selection procedure using Statistica Version 6 for Windows (StatSoft, Inc. 2003). Rarefaction methods using r (v. 2.8.0 for Windows) were used to consider any effects on syrphid sampling success of sampling in different habitat types featuring different vegetation structures. However, the species richness from field samples and the species richness resulting from rarefaction curves, rescaled by the number of individuals, was highly correlated ($P < 0{\cdot}001$). Therefore, the analyses were conducted using the original field data. Data on syrphid densities and quantities of flowers were log-transformed to compensate for the skewness and ⁄ or kurtosis of the data. These models were performed separately for each of the three sampling dates and each of four spatial scales (0·5–4 km radius) of landscape complexity. To test for differences between habitat types post hoc Tukey highest significant differences tests (with P < 0·05 as level of significance) were performed. In addition, we compared regression lines relating total species richness and the abundance of the most abundant syrphid species, *Episyrphus balteatus*, to the proportion of arable land, distinguishing between wheat-fields and adjacent strip habitats. Moreover, species richness and abundance of syrphids were related to the number of flowers per square metre using simple regression models. In the text, arithmetic means ± standard errors are given.

Results

A total of 20 syrphid species and 829 individuals were collected during the three sampling periods. They averaged 1·7 ± 2·0 species and 5·2 ± 11·0 individuals per 100 m transect. The community was dominated by aphidophagous species (1·3 ± 1·5) and individuals (4·2 ± 9·8), followed by syrphids with other larval feeding types such as saprophagous, detrivorous and bacteria-eating, phytophagous and fungivorous species (0·4 ± 0·9) and (0·9 ± 3·6) individuals. The abundance of these trophic groups during the three sampling periods is given in Appendix S3, Supporting Information.

Effects of sown flower strips

Total species richness and abundance differed between sampling dates, and was highest at the wheat milk-ripening stage. Total richness and abundance increased from wheat–wheat boundaries (control; without any strip) through GS to NFS and BFS (Fig. 1). Total species richness and abundance was generally higher within field margin strips compared with adjacent wheat fields (black and white bars in Fig. 1) giving a highly significant site effect (Table 1). Strip type did not affect total species richness and abundance within adjacent wheat fields. Aphidophagous species richness and abundance showed a similar pattern (Fig. 1, Appendix S1, Supporting Information), but at wheat peak-ripening aphidophagous species richness was significantly higher in wheat fields adjacent to BFS (Fig. 1).

The four most abundant syrphid species, the aphidophagous *Episyrphus balteatus*, *Melanostoma* spp. and *Sphaerophoria* spp. and the saprophagous *Syritta pipiens* were analysed separately. The abundance of *E. balteatus* was highest at wheat milk-ripening and was significantly higher in BFS and NFS compared with wheat–wheat boundaries and GS (Fig. 2). The abundance of *Melanostoma* spp. increased from wheat flowering to wheat milk-ripening, and did not respond to strip types on any sampling date (Fig. 2). The abundance of *Sphaerophoria* spp. strongly increased from wheat flowering to wheat milk-ripening and was higher in BFS at wheat flowering; within NFS and BFS at wheat milk-ripening; and within BFS and NFS and GS at wheat peak-ripening (Fig. 2). The abundance of *Syritta pipiens* also increased from wheat flowering to wheat milk-ripening, with no effects of the availability of strip habitats adjacent to wheat fields (Fig. 2).

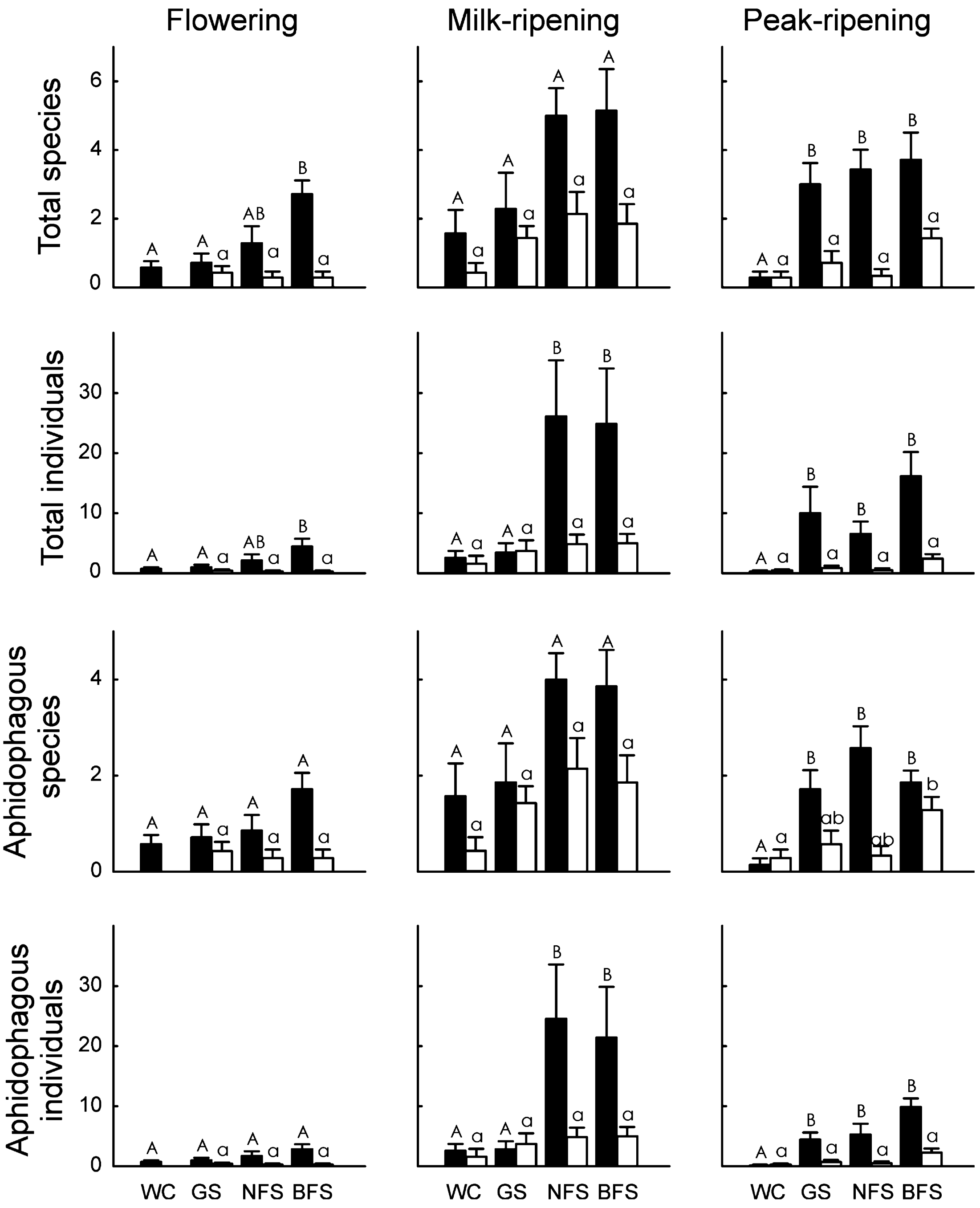

Fig. 1: Total species number and total individual number of syrphids as well as total aphidophagous species number and individual number of aphidophagous syrphids for three consecutive sampling dates at wheat flowering, wheat milk-ripening and wheat peak-ripening (mean numbers and standard deviation is given). Dissimilar capital letters above black bars show significant differences between habitats adjacent to wheat fields, which are grassy strips (GS), narrow flower strips (NFS), broad flower strips (BFS) and wheat–wheat boundary (WC). Dissimilar lower case letters above white bars show significant differences between wheat fields adjacent to the four strip types.

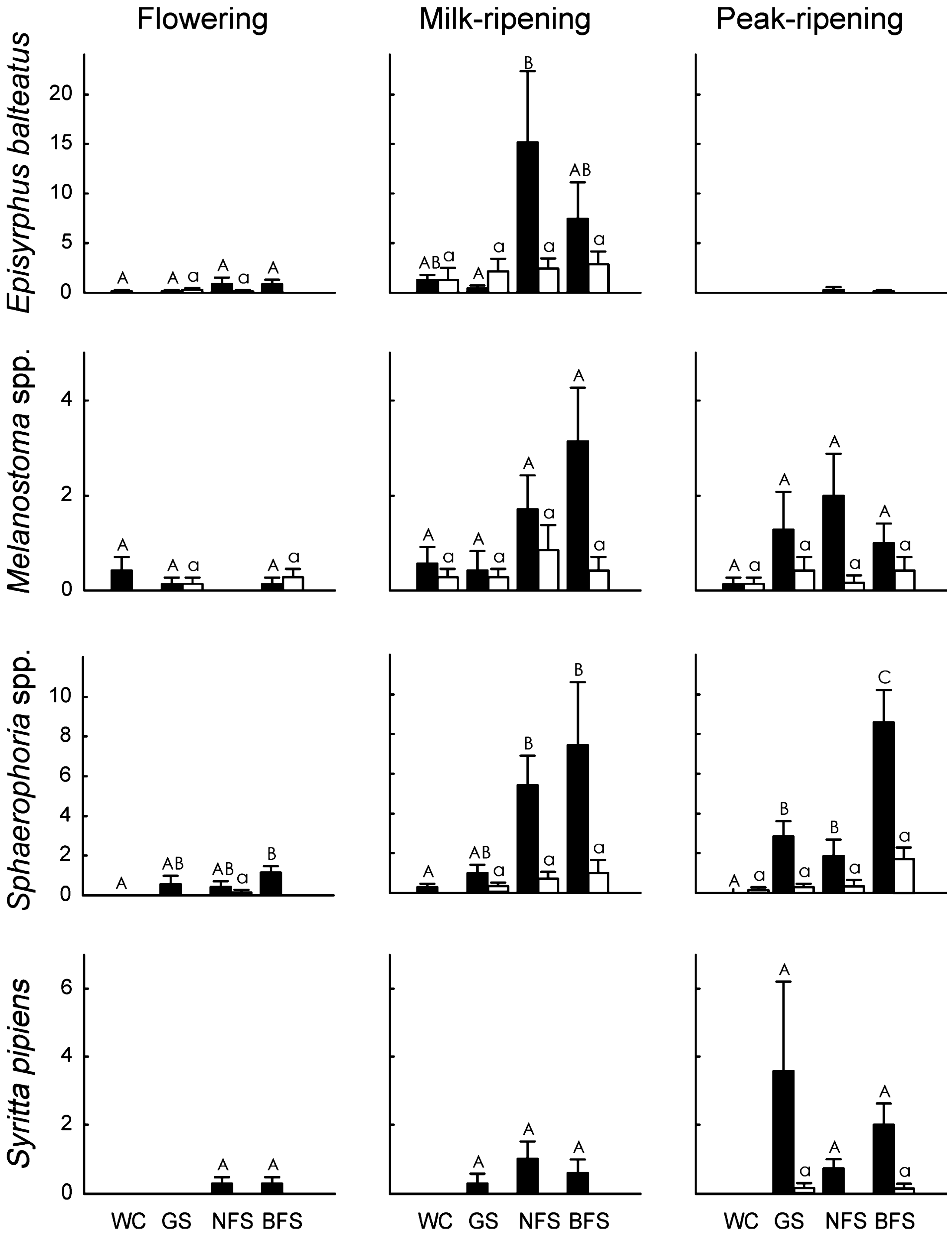

Fig. 2: Total number of individuals of *Episyrphus balteatus*, *Melanostoma* spp., *Sphaerophoria* spp. and *Syritta pipiens* for three consecutive sampling dates at wheat flowering, wheat milk-ripening and wheat peak-ripening (mean number and standard deviation is given). Dissimilar capital letters above black bars show significant differences among habitats adjacent to wheat fields, which are grassy strips (GS), narrow flower strips (NFS), and broad flower strips (BFS) and wheat–wheat boundary (WC). Dissimilar lower case letters above white bars show significant differences between wheat fields adjacent to the four strip types.

Table 1: F-values and levels of significance from general linear models relating syrphid densities to three predictive factors: (i) percentage of arable land per landscape sector; (ii) site, which indicates the dichotomy between strip habitats and adjacent wheat fields; and (iii) habitat type nested in site at wheat flowering, wheat milk-ripening and at wheat peak-ripening at 0·5–4 km scale (radius of landscape sector). Note that the percentage of arable land was positively correlated with total species richness, total number of individuals, total number of aphidophagous species, total number of individuals and *Episyrphus balteatus*, whereas it was negatively correlated with numbers of *Syritta pipiens*.

	Wheat flowering				Wheat milk-ripening Radius of landscape sector (km)				Wheat peak-ripening			
	0·5	1	2	4	0·5	1	2	4	0·5	1	2	4
Total species												
Arable land %	NS	NS	NS	NS	6·0*	7·1*	NS	NS	NS	NS	NS	NS
Site	17·2***	17·2***	17·2***	17·2***	9·1**	9·3**	8·3**	8·3**	37·6***	37·6***	37·6***	37·6***
Habitat type (site)	3·8**	3·8**	3·8**	3·8**	3·7**	3·3**	3·0*	3·0*	9·6***	9·6***	9·6***	9·6***
Model	6·1***	6·1***	6·1***	6·1***	4·3***	4·6***	3·7**	3·7**	13·5***	13·5***	13·5***	13·5***
Total individuals												
Arable land %	NS	NS	NS	NS	8·0**	7·9**	NS	NS	NS	NS	NS	NS
Site	17·6***	17·6***	17·6***	17·6***	8·6**	8·6**	7·5**	7·5**	47·6***	47·6***	47·6***	47·6***
Habitat type (site)	3·2**	3·2**	3·2**	3·2**	5·3***	4·6***	4·0**	4·0**	11·4***	11·4***	11·4***	11·4***
Model	5·7***	5·7***	5·7***	5·7***	5·5***	5·5***	4·5***	4·5***	16·5***	16·5***	16·5***	16·5***
Aphidophagous species												
Arable land %	NS	NS	NS	NS	6·1*	6·5*	NS	NS	NS	NS	NS	NS
Site	8·7**	8·7**	8·7**	8·7**	6·6*	6·6*	5·9*	5·9*	21·2***	21·2***	21·2***	21·2***
Habitat type (site)	NS	NS	NS	NS	3·4**	2·9*	2·6*	2·6*	9·5***	9·5***	9·5***	9·5***
Model	8·7**	8·7**	8·7**	8·7**	3·8**	3·8**	3·1**	3·1**	11·1***	11·1***	11·1***	11·1***
Aphidophagous individuals												
Arable land %	NS	NS	NS	NS	8·3**	7·7**	NS	NS	NS	NS	NS	NS
Site	12·2**	12·2**	12·2**	12·2**	7·5**	7·5**	6·5*	6·5*	36·2***	36·2***	36·2***	36·2***
Habitat type (site)	NS	NS	NS	NS	5·2***	4·5**	4·0**	4·0**	12·0***	12·0***	12·0***	12·0***
Model	12·2**	12·2**	12·2**	12·2**	5·4***	5·3***	4·3***	4·3***	15·3***	15·3***	15·3***	15·3***
Episyrphus balteatus												
Arable land %	NS	NS	NS	NS	18·8***	18·3***	9·7**	9·3**	NS	NS	NS	NS
Site	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Habitat type (site)	NS	NS	NS	NS	3·5**	2·8*	2·4*	2·3*	NS	NS	NS	NS
Model	NS	NS	NS	NS	4·8***	4·7***	3·3**	3·2**	NS	NS	NS	NS
Melanostoma spp.												
Arable land %	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Site	NS	NS	NS	NS	4·1*	4·1*	4·1*	4·1*	5·3*	5·3*	5·3*	5·3*
Habitat type (site)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Model	NS	NS	NS	NS	4·1*	4·1*	4·1*	4·1*	5·3*	5·3*	5·3*	5·3*
Spaerophoria spp.												
Arable land %	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Site	7·7**	7·7**	7·7**	7·7**	14·4***	14·4***	14·4***	14·4***	29·8***	29·8***	29·8***	29·8***
Habitat type (site)	2·8*	2·8*	2·8*	2·8*	3·9**	3·9**	3·9**	3·9**	13·4***	13·4***	13·4***	13·4***
Model	3·6**	3·6**	3·6**	3·6**	5·4***	5·4***	5·4***	5·4***	15·6***	15·6***	15·6***	15·6***
Syritta pipiens												
Arable land %	NS	NS	6·1**	6·6**	NS	NS	NS	NS	NS	NS	NS	NS
Site	NS	NS	NS	NS	6·7*	6·7*	6·7*	6·7*	10·5**	10·5**	10·5**	10·5**
Habitat type (site)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Model	NS	NS	6·1**	6·6**	6·7*	6·7*	6·7*	6·7*	10·5**	10·5**	10·5**	10·5**

***P < 0·001; **P < 0·01; *P < 0·05

Effects of landscape complexity

At wheat milk-ripening stage, total species richness and abundance, and aphidophagous species richness and abundance, correlated positively with the proportion of arable land in adjacent strip habitats occurring within a radius of 0·5–1 km centred on the location of the sites, but not with the proportion of arable land occurring within larger spatial scales (Table 1, Fig. 3). At wheat milk-ripening the abundance of *E. balteatus* correlated positively with the proportion of arable land in adjacent strip habitats occurring within a radius of 0·5–4 km centred on the location of the sites (Table 1, Fig. 3). The abundance of *Melanostoma* spp. and *Sphaerophoria* spp. did not respond to the proportion of arable land at any spatial scale (Table 1). The abundance of Syritta pipiens correlated negatively with the proportion of arable land at spatial scales of 2–4 km at wheat flowering stage (Table 1).

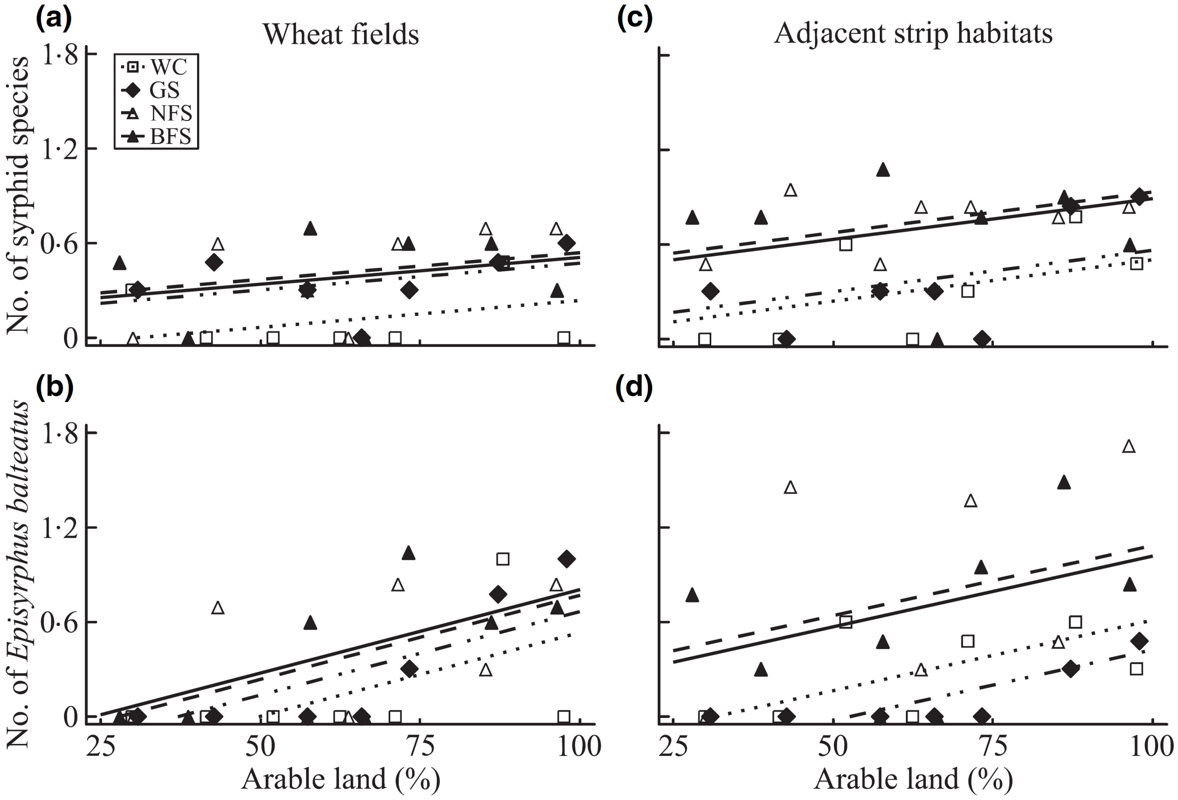

Fig. 3: Total number of syrphid species (no. syrphid species) and number of *Episyrphus balteatus* (no. *Episyrphus balteatus*) in relation to the proportion of arable land (%) at 1 km radius at wheat milk-ripening. Regressions are separated for each type of adjacent strip habitat [WC, wheat–wheat control (blank squares); GS, grassy strip (black squares); NFS, narrow flower strip (blank triangles); BFS, broad flower strip (black triangles)]. All F-ratios and P levels describe differences between intercepts of the regression lines. (a) No. of syrphid species within wheat fields (F-ratio = 2·17, P = 0·119; n = 28). (b) No. *Episyrphus balteatus* within wheat fields (F-ratio: 0·97, P = 0·422; n = 28); (c) No. syrphid species within adjacent strip habitats (F-ratio = 4·06, P = 0·019; n = 28). (d) No. of *Episyrphus balteatus* within adjacent strip habitats (F-ratio = 3·81, P = 0·024; n = 28).

Importance of flower resources

Total species richness and abundance as well as aphidophagous species richness and abundance and species richness and abundance of all other larval feeding types together, were positively correlated with flower densities for each of the three sampling periods, this being strongest at wheat peak-ripening (Fig. 4; statistics in Appendix S4, Supporting Information).

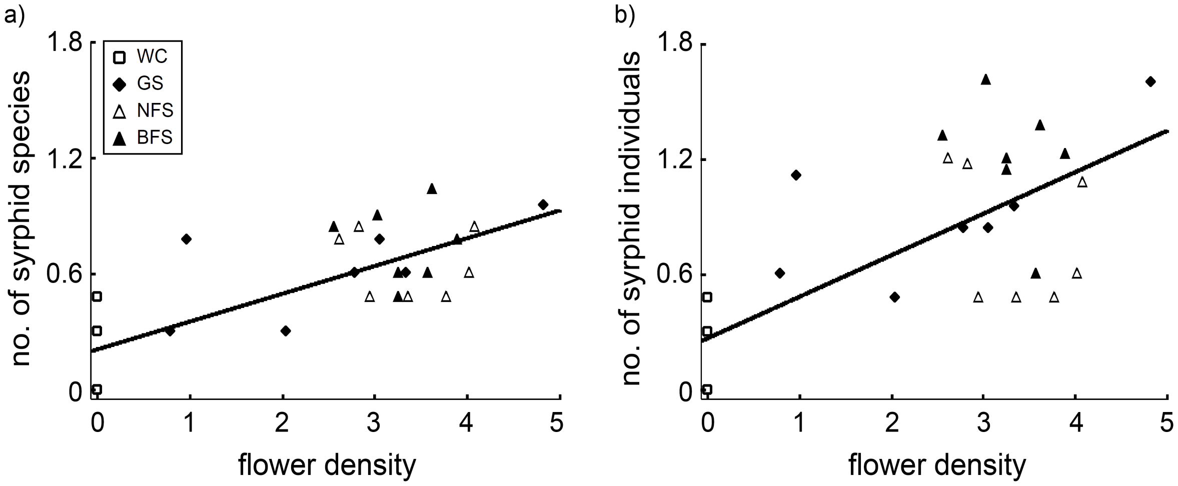

Fig. 4: Flower density in relation to syrphid numbers: (a) log total number of syrphid species (no. syrphid species; F = 33, P = 0·000, n = 28), and (b) log total number of syrphid individuals (no. syrphid individuals; F = 24·6, P = 0·000, n = 18) in relation to flower densities per square metre at wheat peak-ripening (see Appendix S4, Supporting Information for additional results on the relation of number of species and individuals of total syrphids, aphidophagous syrphids and all non-aphidophagous syrphids and flower densities at three consecutive dates). Different symbols indicate the affiliation of the results to a certain strip habitat [WC, wheat–wheat control (open squares), GS, grassy strip (black squares), NFS, narrow flower strip (open triangles), BFS, broad flower strip [(black triangles)].

Discussion

Both narrow and broad flower strips enhanced syrphid densities and particularly the density of aphidophagous species in comparison to grassy strips and wheat–wheat boundaries at the wheat milk-ripening stage. In addition, species richness of aphidophagous syrphids was higher in wheat fields adjacent to broad at wheat peak-ripening stage (when flower density was highest in the strips), indicating a potential spillover across habitats and a positive effect of the broad strips on the potential biocontrol of cereal aphids. Moreover, the number of species and individuals was higher in strips occurring in structurally simple as opposed to complex landscapes. This appeared to be as a result of concentration of syphids in flower strips occurring within structurally simple, intensively managed arable landscapes. This concentration effect was strongest at smaller spatial scales, i.e. within a radius of 0·5–1 km of the study sites.

Aphidophagous syrphids represented the dominant group in all habitat types (similar to the results found by Raskin *et al.* 1992 and Frank 1999), whereas the non-aphidophagous larval feeding types were only found in non-crop habitats, which may be related to better food resource availability in such habitats. Aphidophagous syrphids densities increased from wheat flowering to wheat milk-ripening and then decreased to wheat peak-ripening stage. These temporal changes of aphidophagous syrphids appeared to be associated with the development of aphid colonies within wheat fields, which usually reach their maximum at wheat milk ripening stage and then collapse suddenly (Rabbinge, Ankersmit & Pak 1979).

Syrphids appeared to have profited from the high availability of nectar and pollen resources in sown flower habitats supporting previous findings that flowering weeds attract hoverflies (Schneider 1948; Gilbert 1981; Weiss & Stettmer 1991; Salveter & Nentwig 1993; Bianchi, Booij & Tscharntke 2006). The patch size of flower resources (narrow vs. broad sown strips) did not influence syrphid abundance. This is in contrast to expectations from area-density effects (Steffan-Dewenter & Tscharntke 2000), and suggests that narrow sown flower strips may provide sufficient amounts of pollen and nectar for adult syrphids (Sutherland, Sullivan & Poppy 2001).

Syrphids were hypothesized to profit from a high proportion of semi-natural habitats in structurally complex landscapes, following the patterns exhibited by other pollen and nectar feeding insects in the agricultural landscape (Jonsen & Fahrig 1997; Steffan Dewenter & Tscharntke 1999; Steffan-Dewenter *et al.* 2002; Weibull, Östman & Granqvist 2003). However, we found higher densities of syrphids with an increasing proportion of arable land. This result probably reflects crowding effects on flower resources that are rare in structurally simple landscapes. Such crowding of natural enemies in response to local concentrations of flower resources is little known, but can be expected to exert a high influence on local biodiversity and food web interactions (Thies, Steffan-Dewenter & Tscharntke 2008). Therefore, the opportunistic resource use of syrphids in combination with their high dispersal ability may (temporally) connect isolated habitats in intensified agricultural landscapes. For example, the dominant species, *E. balteatus*, is known to exhibit high mobility with high dispersal rates (Krause & Poehling1996; Lundberg & Moberg 2003; Rand, Tylianakis & Tscharntke 2006; Hondelmann & Poehling

2007). This pattern resembles the situation where social honey bees concentrate in flower patches in simple landscapes based on an opportunistic exploitation of resources at large spatial scales (Steffan-Dewenter *et al*. 2002).

These findings have consequences for the implementation of agri-environment measures for syrphid flies. In complex landscapes, the effects of sown flower strips are hardly visible, whereas in simple landscapes, they are most effective. These results support the general idea that promoting landscape heterogeneity might be economically more efficient in simple landscapes (Roschewitz *et al*. 2005; Tscharntke *et al*. 2005; Holzschuh *et al*. 2007). The species richness and abundance of both total and aphidophagous syrphid species responded to the landscape context at the smallest spatial scales of 0·5–1 km (radius of landscape sector). This result is surprising given the fact that syrphids are highly vagile organisms with excellent vision abilities (Bernard & Stavenga 1979; Lunau & Wacht 1994) easily detecting remote resource patches in monotonous, non-nutritious environments. However, the findings of Harwood *et al*. (1994) suggest that hoverflies are less likely to cross areas with breaks in vegetation ground cover. Furthermore, only small landscape sectors may be expected to become ecologically effective for the concentration effect on patchy resources such as the flower strips. At larger spatial scales these small patches may become increasingly less attractive. An alternative explanation may be that landscapes become more similar when larger sectors are considered, thereby reducing potential explanatory power. However, previous results in the same landscapes showed that bumblebees experienced their surrounding landscape at different spatial scales dependent on their body sizes (from 100 to 3000 m radius, Westphal, Steffan-Dewenter & Tscharntke 2006). Similarly, honey bees responded to landscape resources at spatial scales of 3000 m radius, while solitary bees respond to at scales of just 500 m radius (Steffan-Dewenter *et al*. 2002). These studies provide evidence that these spatial scales (radii from 500 to 4000 m) are biologically meaningful.

Conclusion

Agriculture is a major land-use type in Europe, and the maintenance of biodiversity in agroecosystems is of great importance for ecosystem functioning (Foley *et al*. 2005; Tscharntke *et al*. 2005). Our results show that sown flower strips in agricultural landscapes can enhance the diversity and abundance of syrphid flies, with the potential to improve the biological control of aphid pests. Sown flower strips are therefore an element of current, mainly locally orientated, agri-environmental schemes. However, our results showed that the local importance of sown flower strips is mediated by landscape context. The concentration of syrphid species and individuals in structurally simple landscapes supports the idea that agri-environmental measures are most effective in structurally simple landscapes, with spillover of aphidophagous species from sown flower strips to adjacent wheat fields. Understanding how landscape composition affects the efficiency of environmental measures is important for the optimization of agri-environment schemes, including the value of sown flower strip habitats as sources of beneficial arthropods.

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Appendices

Appendix S1: Syrphid species: mean and standard deviation for three consecutive dates: (i) wheat flowering (wf), (ii) wheat milk-ripening (wmr) and (iii) wheat peak-ripening (wpr).

species	mean ±SD wf	mean ±SD wmr	mean ±SD wpr
Cheilosia spec. [b] (Antiqua G.)	0.000 ± 0.000	0.000 ± 0.000	0.018 ± 0.134
Cheilosia spec. [b] (Bergenstammi G.)	0.107 ± 0.679	0.304 ± 1.747	0.054 ± 0.227
Cheilosia spec. [b] (Canicularis G.)	0.000 ± 0.000	0.018 ± 0.134	0.000 ± 0.000
Episyrphus balteatus [a] (Degeer) 1776	0.304 ± 0.851	4.018 ± 9.114	0.054 ± 0.297
Eristalis abusiva [c] (Collin) 1931	0.018 ± 0.134	0.036 ± 0.267	0.000 ± 0.000
Eristalis abustorum [c] (Linnaeus) 1758	0.018 ± 0.134	0.018 ± 0.134	0.446 ± 2.296
Eristalis jugorum [c] (Egger) 1858	0.000 ± 0.000	0.054 ± 0.227	0.018 ± 0.134
Eristalis pertinax [c] (Scopoli) 1763	0.000 ± 0.000	0.018 ± 0.134	0.000 ± 0.000
Eristalis tenax [c] (Linnaeus) 1758	0.018 ± 0.134	0.000 ± 0.000	0.339 ± 0.920
Eupeodes corollae [a] (Fabricius) 1794	0.125 ± 0.470	0.232 ± 0.687	0.000 ± 0.000
Eupeodes latifasciatus [a] (Macquart) 1829	0.000 ± 0.000	0.018 ± 0.134	0.000 ± 0.000
Helophilus trivittatus [c] (Fabricius) 1805	0.018 ± 0.134	0.018 ± 0.134	0.000 ± 0.000
Melanostoma mellinum [a] (Linnaeus) 1758	0.000 ± 0.000	0.250 ± 0.796	0.000 ± 0.000
Melanostoma scalare [a] (Fabricius) 1794	0.000 ± 0.000	0.268 ± 0.820	0.000 ± 0.000
Melanostoma spec [a] (Schiner) 1860	0.125 ± 0.334	0.893 ± 1.723	0.679 ± 1.390
Platycheirus albimanus [a] (Fabricius) 1781	0.000 ± 0.000	0.018 ± 0.134	0.000 ± 0.000
Platycheirus angustatus [a] (Zetterstedt) 1843	0.000 ± 0.000	0.018 ± 0.134	0.036 ± 0.187
Platycheirus clypeatus [a] (Meigen) 1822	0.000 ± 0.000	0.089 ± 0.345	0.089 ± 0.438
Platycheirus europaeus [a] (Goeldlin, Maibach & Speight) 1990	0.000 ± 0.000	0.018 ± 0.134	0.000 ± 0.000
Platycheirus fluviventris [a] (Macquart) 1829	0.000 ± 0.000	0.000 ± 0.000	0.018 ± 0.134
Platycheirus spec. [a] (Lepeletier & Serville) 1828	0.018 ± 0.134	0.232 ± 0.539	0.054 ± 0.227
Sphaerophoria spec. [a] (Lepeletier & Serville) 1828	0.286 ± 0.680	2.000 ± 4.260	1.964 ± 3.330
Syritta pipiens [b] (Linnaeus) 1758	0.071 ± 0.260	0.232 ± 0.738	0.821 ± 2.797
Syrphus ribesii [a] (Linnaeus) 1758	0.000 ± 0.000	0.054 ± 0.297	0.000 ± 0.000
Syrphus vittripennis [a] (Meigen) 1822	0.018 ± 0.134	0.018 ± 0.134	0.018 ± 0.134
Xanthogramma laetum [a] (Fabricius) 1794	0.018 ± 0.134	0.000 ± 0.000	0.000 ± 0.000

[a] aphidophagous; [b] saprophagous; [c] detrivorus and bacteria-eating

Appendix S2: Plant species recorded during transect walks at wheat flowering (wf), wheat milk-ripening (wmr) and wheat peak-ripening (wpr).

species	mean ± SD wf	mean ± SD wmr	mean ± SD wpr
Achillea millefolium [b] L. (Asteraceae)	0.097 ± 0.496	0.229 ± 0.826	0.346 ± 1.099
Anchusa officinalis [b] L. (Boraginaceae)	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
Anthriscus sylvestris [a] L. (Apiaceae)	0.213 ± 0.840	0.366 ± 1.033	0.761 ± 1.389
Borago officinalis [a] L. (Boraginaceae)	0.000 ± 0.000	0.241 ± 0.470	0.177 ± 0.390
Brassica oleracea [a] L. (Brassicaceae)	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
Calendula arvensis [a] L. (Asteraceae)	0.000 ± 0.000	0.040 ± 0.167	0.000 ± 0.000
Campanula rapunculoides [a] L. (Campanulaceae)	0.000 ± 0.000	0.000 ± 0.000	0.147 ± 0.452
Carum carvi [a] L. (Apiaceae)	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
Centaurea cyanus [b] L. (Asteraceae)	0.000 ± 0.000	0.019 ± 0.099	0.000 ± 0.000
Chrysanthemum leucanthemum [a] L.(Asteraceae)	0.747 ± 1.081	0.396 ± 0.654	0.164 ± 0.381
Cichorium intybus [a] L. (Cichorioidae)	0.000 ± 0.000	0.079 ± 0.285	0.000 ± 0.000
Cirsum arvense [b] L. (Asteraceae)	0.033 ± 0.166	0.404 ± 0.698	0.753 ± 0.814
Convolvulus arvensis [b] L. (Convolvulaceae)	0.009 ± 0.048	0.278 ± 0.621	0.000 ± 0.000
Daucus carota [b] L. (Apiaceae)	0.000 ± 0.000	0.155 ± 0.803	0.000 ± 0.000
Epilobium spp. [b] L. (Onagraceae)	0.135 ± 0.688	0.187 ± 0.409	0.000 ± 0.000
Fagopyrum esculentum [a] MOENCH (Polygonaceae)	0.000 ± 0.000	0.055 ± 0.287	0.000 ± 0.000
Foeniculum vulgare [a] MILL. (Apiaceae)	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
Galium aparine [b] L. (Rubiaceae)	0.103 ± 0.362	0.000 ± 0.000	0.000 ± 0.000
Galium spp. [b] L. (Rubiaceae)	0.061 ± 0.311	0.000 ± 0.000	0.000 ± 0.000
Geranium dissectum [b] L. (Geraniaceae)	0.137 ± 0.396	0.059 ± 0.181	0.000 ± 0.000
Glechoma hederacea [b] L. (Lamiaceae)	0.036 ± 0.182	0.000 ± 0.000	0.000 ± 0.000
Helianthus annuus [a] L. (Asteraceae)	0.000 ± 0.000	0.000 ± 0.000	0.037 ± 0.112
Heracleum sphondylium [b] L. (Apiaceae)	0.000 ± 0.000	0.136 ± 0.707	0.000 ± 0.000
Hypericum perforatum [a] L. (Hypericaceae)	0.033 ± 0.166	0.155 ± 0.358	0.264 ± 0.490
Isatias tinctoria [a] L. (Brassicaceae)	0.051 ± 0.260	0.000 ± 0.000	0.000 ± 0.000
Lamium album [b] L. (Lamiaceae)	0.090 ± 0.258	0.057 ± 0.295	0.077 ± 0.305
Lepidium sativum [a] L. (Brassicaceae)	1.336 ± 1.649	0.306 ± 0.782	0.000 ± 0.000
Linum usitatissimum [a] L. (Linaceae)	0.000 ± 0.000	0.078 ± 0.293	0.014 ± 0.075
Lotus corniculatus [b] L. (Fabaceae)	0.041 ± 0.208	0.354 ± 1.027	0.000 ± 0.000
Matricaria recutita [b] L. (Asteraceae)	0.348 ± 0.726	0.489 ± 0.896	0.434 ± 0.753
Matricaria spp. [b] L. (Asteraceae)	0.000 ± 0.000	0.184 ± 0.474	0.000 ± 0.000
Medicago lupulina [b] L. (Fabaceae)	0.332 ± 0.940	0.000 ± 0.000	0.000 ± 0.000
Medicago sativa [a] L. (Fabaceae)	0.000 ± 0.000	0.059 ± 0.305	0.076 ±0.403
Meliotus albus [a] MED. (Fabaceae)	0.148 ± 0.586	0.563 ± 1.216	0.872 ± 1.551
Meliotus officinalis [a] L. (Fabaceae)	0.098 ± 0.502	0.802 ± 1.292	0.703 ± 1.334
Myosotis arvensis [b] L. (Boraginaceae)	0.568 ± 0.993	0.300 ± 0.744	0.000 ± 0.000
Nigella sativa [a] L. (Ranunculaceae)	0.000 ± 0.000	0.059 ± 0.305	0.000 ± 0.000

[a] sown crop and wild plants (seed mixture); [b] not contained in the seed mixture. *(continued)*

Appendix S2: Plant species recorded during transect walks at wheat flowering (wf), wheat milk-ripening (wmr) and wheat peak-ripening (wpr) (continued).

species	mean ± SD wf	mean ± SD wmr	mean ± SD wpr
Papaver rhoeas [a] L. (Papaveraceae)	0.084 ± 0.199	0.209 ± 0.337	0.142 ± 0.329
Pastinaca sativa [a] L. (Apiaceae)	0.000 ± 0.000	0.076 ± 0.397	0.000 ± 0.000
Phacelia tanacetifolia [a] BENTH. (Hydrophyllaceae)	0.982 ± 1.493	1.063 ± 1.456	0.450 ± 0.887
Pisum sativum [a] L. (Fabaceae)	0.000 ± 0.000	0.100 ± 0.332	0.022 ± 0.114
Plantago lanceolata [b] L. (Plataginaceae)	0.000 ± 0.000	0.036 ± 0.186	0.000 ± 0.000
Ranunculus spp. [b] L. (Ranunculaceae)	0.079 ± 0.305	0.009 ± 0.047	0.000 ± 0.000
Raphanus sativus [a] L. (Brassicaceae)	0.646 ± 1.037	0.769 ± 1.126	0.343 ± 0.709
Sinapis alba [a] L. (Brassicaceae)	0.980 ± 1.241	0.462 ± 0.901	0.212 ± 0.563
Stellaria spp. [b] L. (Caryophyllaceae)	0.153 ± 0.564	0.089 ± 0.332	0.000 ± 0.000
Tanacetum vulgare [a] L. (Asteraceae)	0.000 ± 0.000	0.443 ± 0.872	0.698 ± 1.135
Trifolium pratense [b] L. (Fabaceae)	0.000 ± 0.000	0.064 ± 0.331	0.000 ± 0.000
Trifolium repens [b] L. (Fabaceae)	0.049 ± 0.144	0.296 ± 0.577	0.106 ± 0.321
Veronica persica [b] POIR. (Scrophulariaceae)	0.079 ± 0.288	0.000 ± 0.000	0.000 ± 0.000
Vicia spp. [b] L. (Fabaceae)	0.191 ± 0.707	0.076 ± 0.395	0.000 ± 0.000
Viola spp. [b] L. (Violaceae)	0.055 ± 0.214	0.000 ± 0.000	0.000 ± 0.000

[a] sown crop and wild plants (seed mixture); [b] not contained in the seed mixture.

Appendix S3: Mean numbers, minima and maxima of species and individuals for (i) total syrphids, (ii) aphidophagous syrphids and (iii) syrphids with other feeding types at three consecutive dates. Mean numbers and standard deviation is given.

	mean + SE	min	max
wheat flowering			
number of all species	0.898 ± 1.160	0	4
number of all individuals	1.327 ± 0.321	0	12
number of aphidophagous species	0.694 ± 0.114	0	3
number of aphidophagous individuals	1.041 ± 0.220	0	7
number of species (other larval feeding type)	0.204 ± 0.077	0	2
number of individuals (other larval feeding type)	0.286 ± 0.124	0	5
wheat milk-ripening			
number of all species	2.482 ± 0.340	0	11
number of all individuals	9.018 ± 2.114	0	75
number of aphidophagous species	2.143 ± 0.260	0	6
number of aphidophagous individuals	8.321 ± 1.959	0	72
number of species (other larval feeding type)	0.339 ± 0.126	0	6
number of individuals (other larval feeding type)	0.696 ± 0.354	0	19
wheat peak-ripening			
number of all species	1.673 ± 0.249	0	7
number of all individuals	4.709 ± 1.092	0	39
number of aphidophagous species	1.109 ± 1.153	0	4
number of aphidophagous individuals	2.982 ± 0.554	0	14
number of species (other larval feeding type)	0.564 ± 0.151	0	5
number of individuals (other larval feeding type)	1.727 ± 0.734	0	30

Appendix S4: Blossom densities per square metre in relation to species richness and abundance of (i) total syrphids, (ii) aphidophagous syrphids and (iii) syrphids with other larval feeding type.

	function	*F*	*P*	r
total syrphids				
wheat flowering				
no. of individuals	Y = 0.09 X + 0.23	9.4	0.005	0.516
no. of species	Y = 0.07 X + 0.21	9.8	0.004	0.524
wheat milk-ripening				
no. of individuals	Y = 0.18 X + 0.52	7.7	0.010	0.477
no. of species	Y = 0.11 X + 0 40	7.5	0.011	0.473
wheat peak-ripening				
no. of individuals	Y = 0.22 X + 0.27	24.6	0.000	0.697
no. of species	Y = 0.14 X + 0.21	33.8	0.000	0.752
aphidophagous syrphids				
wheat flowering				
no. of individuals	Y = 0.06 X + 0.24	6.2	0.019	0.440
no. of species	Y = 0·04 X + 0.22	4.6	0.042	0.387
wheat milk-ripening				
no. of individuals	Y = 0.17 X + 0.52	7.3	0.012	0.468
no. of species	Y = 0.09 X + 0.40	6.8	0.015	0.445
wheat peak-ripening				
no. of individuals	Y = 0.17 X + 0.25	16.4	0.000	0.622
no. of species	Y = 0.11 X + 0.20	19.2	0.000	0.652
all non-aphidophagous				
wheat flowering				
no. of individuals	Y = 0.06 X - 0.02	8.5	0.007	0.496
no. of species	Y = 0.05 X - 0.02	10.1	0.004	0.529
wheat milk-ripening				
no. of individuals	Y = 0.08 X + 0.01	5.3	0.030	0.410
no. of species	Y = 0.06 X + 0.01	6.1	0.021	0.435
wheat peak-ripening				
no. of individuals	Y = 0.16 X - 0.01	11.8	0.002	0.559
no. of species	Y = 0.10 X + 0.01	12.9	0.001	0.576

CHAPTER 3

Regionally and temporally contrasting responses of aphidophagous and non-aphidophagous syrphid flies to agricultural intensification in north and central Europe

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Abstract

1. Species richness and abundance of aphidophagous and non-aphidophagous syrphid flies can vary largely across geographical regions and landscapes owing to variation in land use, landscape structure, and climate, thereby affecting ecosystem services such as biological pest control.

2. Syrphid flies are among the largest groups of dipterans, with aphidophagous and non-aphidophagous larval feeding types (including agro-ecologically important functional groups) and pollinating adults. We analysed syrphid fly communities of Sweden and Germany in cereal fields under low levels of agricultural intensification (located in structurally complex landscapes) vs. high levels of agricultural intensification (located in structurally simple landscapes).

3. Syrphid fly abundance varied largely between regions, and across seasons. Aphidophagous, but not non-aphidophagous syrphid abundance was higher in Germany than Sweden. In Germany, but not Sweden, aphidophagous syrphid species were more abundant at high levels of agricultural intensification, providing large cereal aphid resources, whereas non-aphidophagous species were more abundant at low levels of agricultural intensification in both regions, obviously benefiting from resources outside cropland. Interestingly, aphidophagous syrphid populations appeared to be synchronized with aphid occurrence only in Germany, not Sweden. Such region-specific changes in temporal synchronisation are little recognized, but may be of great functional importance. Future agri-environmental management should therefore consider the regionally and temporally contrasting responses of functional syrphid groups, and the region-specific variation in their potential to suppress aphids.

Key-words: *Syrphidae, agricultural intensification, landscape context, farming practices, biodiversity, biological control of cereal aphids*

Introduction

Modern European agriculture is predominantly associated with intensified land use practices including the application of mineral fertilizers and pesticides (Papendick *et al.* 1986; Biswas 1994; Tilman *et al.* 2002), and this is often accompanied by the loss and fragmentation of semi-natural habitats, leading to homogenous agricultural landscapes (Robinson & Sutherland 2002). Landscape simplification has been shown to result in a decrease of biodiversity and related ecosystem services such as biological pest control (Tews *et al.* 2004; Chaplin-Kramer *et al.* 2011). Organic farming practices at local scales and a high habitat diversity at landscape scales have been shown to enhance local biodiversity (Bengtsson *et al.* 2005). Such landscape matrix effects can mitigate negative effects of local agricultural intensification on biodiversity, including natural enemies contributing to biological control (Jeanneret *et al.* 2003; Schmidt *et al.* 2005; Tscharntke *et al.* 2005; Bianchi *et al.* 2006; Chaplin-Kramer *et al.* 2011).

Cereal aphids (Hemiptera: *Aphididae*) are economically important pest insects that are attacked by several species of natural enemies. Recent enemy exclusion experiments suggest additive or even synergistic effects of natural enemies (Schmidt *et al.* 2003; Holland *et al.* 2008; Thies *et al.* 2011), with aphid-eating syrphid larvae contributing to the suppression of cereal aphid outbreaks (Chambers & Adams 1986; Tenhumberg & Poehling 1995; Brewer & Elliott 2004). However, functional enemy groups can respond differentially to environmental changes, with temporally variable responses (Teodoro *et al.* 2009). The large-scale context of functional biodiversity has been little studied so far, but is important to goal setting in landscape management (Östman *et al.* 2001; Lang 2003; Tscharntke & Brandl 2004; Roschewitz *et al.* 2005; Thies *et al.* 2011).

Syrphid flies (Diptera: Syrphidae) represent one of the largest groups of dipterans, with over 800 phytophagous, saprophagous and zoophagous species occurring in Europe (Oosterbroek *et al.* 2006). Habitat requirements of syrphid flies are related to the availability of larval food resources. Aphidophagous species occur in a wide range of habitat types including crop fields harbouring aphid pests, while species with other larval feeding types appear to be more restricted to non-crop habitats (Frank 1999). Adult syrphid flies are known to benefit from floral resources provided by diversified landscapes with high proportions of semi-natural habitats or introduced flower habitats (Hickman & Wratten 1996; Haenke *et al.* 2009). Region-specific features of landscape structures, farming practices, weather and climate can therefore filter species-specific traits of syrphid species in biogeographical regions (Östman *et al.* 2001; Roschewitz *et al.* 2005; Thies *et al.* 2005).

In this study we analysed species richness and abundance of adult syrphid flies grouped by their larval feeding type (aphidophagous vs. non-aphidophagous) communities in contrasting regions (Sweden and Germany) and landscapes (with low versus high levels of agricultural intensification). Syrphid flies are highly mobile organisms, and therefore, can contribute to the sustainability and preservation of ecosystem services such as biocontrol and pollination in intensified agricultural landscapes. We hypothesized that (i) species richness and abundance of syrphid flies are higher and peak earlier in the season in the southern region (Germany) owing to more favourable climatic conditions and that (ii) abundance of aphidophagous syrphids are higher in intensively managed landscapes with high proportions of crop fields due to higher larval food availability, while (iii) non-aphidophagous syrphids benefit from landscapes with low levels of agricultural intensification owing to food resources outside cropland.

Materials and methods

Study area & experimental design

We analysed adult syrphid fly diversity and abundance in cereal fields of two European regions (summer barley in Sweden, n = 8 and winter wheat in Germany, n = 8). Samplings were temporally synchronized according to phenological growth stages of cereals. In each region we selected four fields located in structurally complex landscapes at low level of agricultural intensification (low level of AI), and high proportions of semi-natural habitats (over 30% in 1 km radii) and four fields located in structurally simple landscapes at high level of AI with high proportions of arable land (over 90 %). In Germany, fields with low level of AI were organically managed (no application of mineral fertilizers and pesticides) and fields with high level of AI were conventionally managed (with standard application regimes of mineral fertilizers and chemical pesticides), thus agricultural intensification at the local field and the landscape scale was varied simultaneously (for further information on the study sites see Geiger et al 2010). Percent arable land per landscape sector has been shown to be closely and negatively related to habitat-type diversity, indicating high landscape complexity (Batáry *et al.* 2011).

Sampling of syrphids flies

We captured syrphids using coloured pan-traps along a 60 m transect located at a distance of 10-12 m to the edge of each field. In total six pan-traps of three colours (yellow, n = 2; white, n =2 and blue, n = 2, to meet colour preferences of syrphids species) per cereal field were randomly installed at a distances of 10 meters from each other. The traps were attached to wooden slats and vertically adjusted to the height of the cereal plants during the season. Each trap was filled with 500 ml of water and glycol (1:4) plus a drop of a detergent to diminish surface tension. Installations were exposed for one week. Sampling was carried out during four dates (from early to late cereal flowering in May-2008 to early and late cereal milk-ripening in June/July-2008). Samples were separated from water and glycol, transferred to 70 % alcohol solutions in the field, and taken to the laboratory. Syrphid species were separated from all other arthropod genera and identified to the species level using identification keys (van Veen 2004). Syrphid species from pantraps were pooled per site. Species were sorted into two trophic groups according to their larval feeding type: aphidophagous feeding type and a combined group of all non-aphidophagous larval feeding types (phytophagous and saprophagous).

Statistical analyses

Total syrphid fly diversity and abundance as well as diversity and abundance of trophic groups (aphidophagous group vs. non-aphidophagous), and those of single syrphid species were analysed by Linear Mixed Effect Models, using *log*(x + 1)-transformed count data and variance functions to model heteroscedasticity in the lme package of R 2.12.0 (R Development Core Team 2010). We analysed the factors region (Sweden vs. Germany), level of agricultural intensification, (low vs. high levels of AI) and date (during early and late cereal flowering and during early and late cereal milk-ripening), and up to third order interactions of these factors. In each model, field-ID (1-8) grouped by date was added as an error level. We thereby took into account the temporal nestedness of the samplings within a field. Model assumptions were tested by examining the Gaussian distribution of the residuals. Moreover, we tested for temporal autocorrelation among sampling dates by analysing model residuals with the R package “nlme” (Pinheiro *et al.* 2010). Minimal adequate models were found by using backward selection procedure based on Maximum

Likelihood (Crawley 2007). Differences between regions as well as low versus high levels of agricultural intensification were analysed by comparing confidence intervals of estimators for factor levels. Abundance and species richness of functional groups were positively correlated (Total species richness: r= 0.8, p= <0·001; Aphidophagous species richness: r= 0.9, p= <0·001; Non-aphidophagous richness: r= 0.8, p= <0·001), and therefore included in the models as covariate in the analyses of species richness patterns. In the text means and standard errors are given.

Results

In total, 39 syrphid species with 3198 individuals were collected during the four sampling periods. They averaged 4.4 ± 0.3 species and 50.0 ± 9.8 individuals per 60 m transect. Syrphid communities were dominated by aphidophagous species (3.3 ± 0.2) and individuals (47.8 ± 9.8), followed by non-aphidophagous species (1.0 ± 0.2) and individuals (2.2 ± 0.5). The most abundant aphidophagous syrphid species were *Episyrphus balteatus* (1856 individuals), *Eupeodes corollae* (671 individuals) and *Sphaerophoria scripta* (381 individuals), with highest relative abundance of *E. balteatus* in German study sites and highest relative abundance of *S. scripta* in Swedish study sites (for total syrphid numbers across the four sampling periods, see Appendix S1).

Total species richness and abundance

Total syrphid species richness (Tab.A, Fig.1: A-D) differed between regions, peaking in Sweden at late milk-ripening stage (5.3 ± 0.8), and in Germany at early milk-ripening stage (6.6 ± 0.7) (interaction: region × date). Total syrphid species richness was higher at low levels of agricultural intensification (4.8 ± 0.4 vs. 4.0 ± 0.4), with stronger effects in Sweden (interaction: level of AI × region). Total syrphid abundance (Tab.A, Fig.1: E-H) was more than 7-times higher in Germany (87.5 ± 17.0) compared to Sweden (12.4 ± 2.7), and was higher at high levels of agricultural intensification (62.0 ± 17.8 vs. 38.0 ± 7.9), with stronger effects in Germany (interaction: level of AI × region).

Species richness and abundance of aphidophagous syrphids

Aphidophagous syrphid species richness (Tab.A, Fig.1: I-L) differed between regions peaking at late milk-ripening stage (3.9 ± 0.5) in Sweden, and at early milk-ripening stage (5.4 ± 0.5) in Germany (interaction: region × date). Aphidophagous syrphid species richness was not affected by AI. Aphidophagous syrphid abundance (Tab.A, Fig.1: M-P) was more than 8 times higher in Germany (85.6 ± 17.1) compared to Sweden (10.1 ± 2.4), with higher abundances at high levels of agricultural intensification (61.4 ± 17.8 vs. 34.3 ± 7.8), and positive effects of AI particularly in Germany (interaction: level of AI × region).

Species richness and abundance of non-aphidophagous syrphids

Non-aphidophagous syrphid species richness (Tab.A, Fig.1: Q-T) did not differ between regions and was not affected by the levels of AI, but across sampling dates, peaking at early cereal flowering (1.0 ± 0.2). Non-aphidophagous syrphid abundance (Tab.A, Fig.1: U-X) differed between regions, peaking in Sweden at late milk-ripening stage (4.9 ± 3.1) and in Germany at early milk-ripening stage (2.9 ± 1.3) (interaction: region × date). Non-aphidophagous syrphid abundance was more than 5 times higher at low levels of AI (3.7 ± 0.9 vs. 0.6 ± 0.2).

Table A: Linear mixed models relating species richness and abundance of total, aphidophagous and non-aphidophagous syrphids flies as well as the abundance of the three most frequent species. *Note:* The predictive factors are region (Sweden, Germany), level of AI (low or high levels of agricultural intensification, AI) and date (1-4; date). Denominator degrees of freedom (*DDF*), *F*-values and *P*-values are given.

		DDF	F	p
Total species	total individuals	45	132.4	<0.001
	region	12	0.1	NS
	level of AI	12	5.4	<0.05
	date	45	2.2	NS
	region × date	45	9.3	<0.01
	level of AI × region	12	7.7	<0.05
Total individuals	region	12	197.8	<0.001
	level of AI	12	7.7	<0.05
	date	45	26.1	<0.001
	level of AI × region	12	7.8	<0.05
Aphidophagous species	aphidophagous individuals	45	200.5	<0.001
	region	14	1.2	NS
	date	45	7.8	<0.01
	region × date	45	10.4	<0.01
Aphidophagous individuals	region	12	200.7	<0.001
	level of AI	12	16.2	<0.01
	date	47	24.9	<0.001
	level of AI × region	12	6.6	< 0.05
Non-aphidophagious species	non-aphidophagous individuals	46	217.7	<0.001
	date	46	5.8	<0.05
Non- aphidophagious individuals	region	13	0.1	NS
	level of AI	13	11.2	<0.01
	date	46	0.0	NS
	region × date	46	7.1	<0.05
Episyrphus balteatus	region	12	521.2	<0.001
	level of AI	12	8.6	<0.05
	date	45	192.1	<0.001
	region × date	45	158.3	<0.001
	level of AI × region	12	3.8	NS
	level of AI × date	45	1.8	NS
Eupeodes corollae	region	12	30.7	<0.001
	level of AI	12	11.5	<0.01
	date	46	4.9	<0.05
	region × date	46	4.5	<0.05
	level of AI × region	12	11.2	<0.01
Sphaerophoria scripta	region	12	9.8	<0.01
	level of AI	12	49.5	<0.001
	date	46	2.2	NS
	region × date	46	7.4	<0.01
	level of AI × region	12	16.3	<0.01

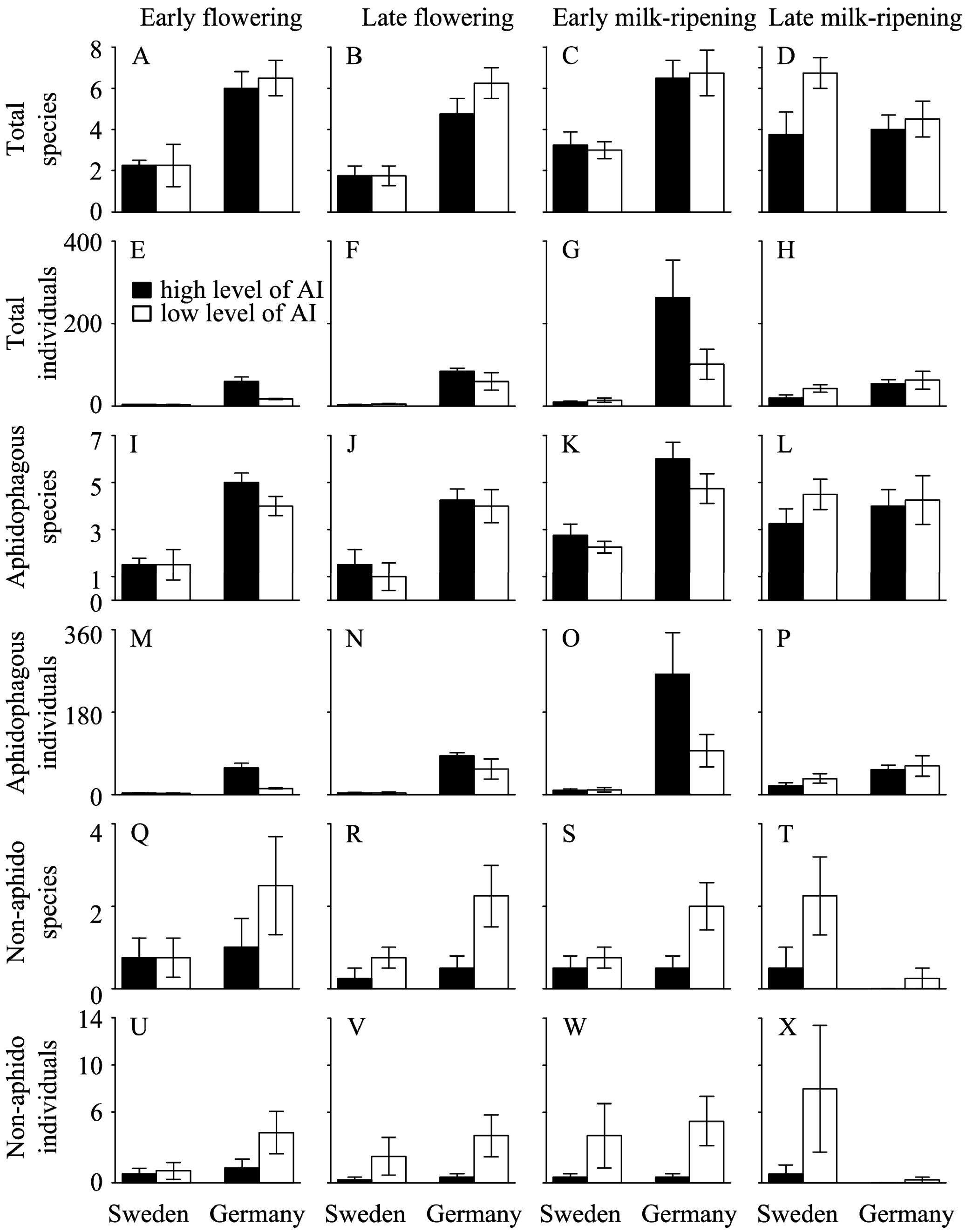

Fig.1: Species richness and abundances in Sweden and Germany of total, aphidophagous and non-aphidophagous syrphid flies (with other larval feeding types) at high levels of AI (black bars) and low levels of AI (white bars) at four consecutive sampling dates during early cereal flowering (1st column), late cereal flowering (2nd column), early cereal milk-ripening (3rd column) and late cereal milk-ripening (4th column). Means and standard errors are given.

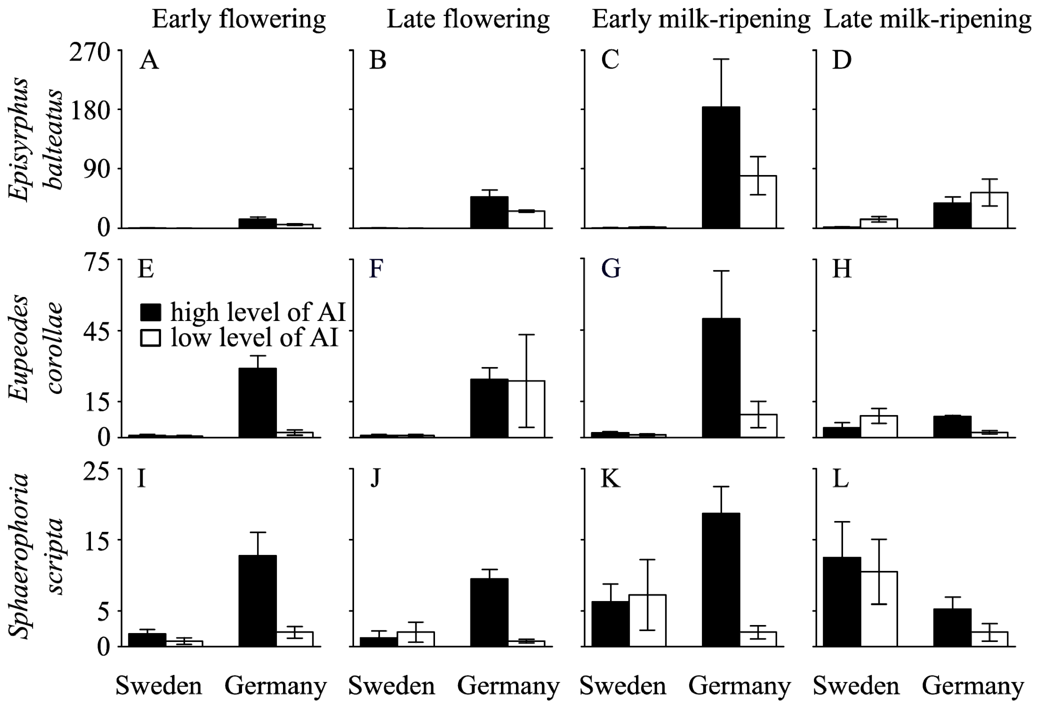

Fig. 2: Abundance of *Episyrphus balteatus*, *Eupeodes corollae* and *Sphaerophoria scripta in* Sweden and Germany at high levels of AI (black bars) and low levels of AI (white bars) at four consecutive sampling dates during early cereal flowering (1st column), late cereal flowering (2nd column), early cereal milk-ripening (3rd column) and late cereal milk-ripening (4th column). Means and standard errors are given.

The three most abundant species

Abundance of the aphidophagous *Episyrphus balteatus* (Tab.A, Fig.2: A-D) was more than 26 times higher in Germany compared to Sweden (Germany: 55.9 ± 13.2 vs. Sweden: 2.1 ± 0.9), peaking at late milk-ripening (7.3 ± 2.9) in Sweden and at early milk-ripening (131.5 ± 41.4) in Germany (interaction: region × date), with higher values at high levels of agricultural intensification (35.6 ± 13.3 vs. 22.4 ± 6.3).

Abundance of the aphidophagous *Eupeodes corollae* (Tab.A, Fig.2: E-H) was more than 8 times higher in Germany compared to Sweden (18.7 ± 4.3 vs. 2.3 ± 0.7) and more than 2 times higher at high levels of agricultural intensification (14.9 ± 3.8 vs. 6.1 ± 2.6), peaking at late milk-ripening (6.5 ± 2.0) in Sweden and early milk-ripening (29.6 ± 12.3) in Germany (interaction: region × date). The positive effect of AI on *E. corollae* differed between regions.

The abundance of the aphidophagous *Sphaerophoria scripta* (Tab.A, Fig.2: I-L) was higher in Germany compared to Sweden (6.6 ± 1.3 vs. 5.3 ± 1.3), peaking at late milk ripening (11.5 ± 3.2) in Sweden and early milk-ripening (10.4 ± 3.6) in Germany, with highest values at high levels of agricultural intensification (8.5 ± 1.3 vs. 3.4 ± 1.0), particularly in Germany (11.6 ± 1.8 vs. 1.7 ± 0.4) (interaction: level of AI ×region).

Discussion

The analyses of the two functional syrphid fly groups showed that species richness and abundance of syrphid flies is higher in southern (Germany) compared to northern (Sweden) regions of Europe. Total abundance was higher at high levels of AI, while total species richness was higher at low levels of AI. Aphidophagous syrphid abundance (but not aphidophagous species richness) was higher at high levels of agricultural intensification, while non-aphidophagous syrphid abundances were higher at low levels of agricultural intensification. Interestingly, abundant aphidophagous syrphid populations only coincide with aphid pests in Germany, but not in Sweden. Region-specific changes in temporal synchronisation of aphidophagous syrphid species and their aphid prey are little studied, but appear to be important for the success of biological control of cereal aphids.

Adult syrphid communities caught in both study regions were dominated by aphidophagous species, which have been shown to be spatially and temporally closely linked to their larval food resources (Tenhumberg & Poehling 1995). Cereal aphid pests usually reach their maximum at cereal milk-ripening stage of the crop (Rabbinge *et al.* 1979), which co-occurs with the highest species richness and abundance of aphidophagous syrphids. Timing and size of early spring migrations of cereal aphids are vastly determined by temperature conditions during winter time, which can result in earlier and stronger aphid infestations at more southern latitudes (Turl 1980; Walters & Dewar 1986). Higher winter temperatures in Germany may be a reason for the earlier occurrence of aphid prey, and comparatively high abundances of aphidophagous syrphid flies overlapping with aphids' peak. This temporal synchronization may be of importance for biological aphid control (Thies *et al.* 2011). Aphidophagous syrphids do apparently not suffer from dispersal limitation in structurally simple landscapes (Jauker *et al.* 2009). Their densities appear rather to be determined by huge aphid populations provided by intensively managed cereal fields.

Moreover, relative abundances of aphidophagous syrphid species changed regionally, with *Episyrphus balteatus* being most abundant in Germany and *Sphaerophoria scripta* being the most abundant species in Sweden (Lundberg & Moberg 2003; Hondelmann & Poehling 2007). Apparently, such region-specific differences in species identity can have consequences for biological aphid control. In our study, the dominating aphidophagous syrphid species in Germany, *E. balteatus*, overwinters as adult. This is why this species is expected to be negatively affected by low temperatures (Hart & Bale 1997) and more dominant in Germany compared to northern regions such as Sweden. Overwintering of adults of *E. balteatus* with relatively early appearance in the season may thereby lead to a better synchronization with their larval prey, contributing to enhanced biological aphid control in Germany (Tenhumberg & Poehling 1995, Keil *et al.* 2008). Contrastingly, the dominating aphidophagous species in Sweden, *Sphaerophoria scripta*, overwinters as larva, pupates in spring and its seasonal appearance is later.

In contrast, non-aphidophagous syrphids (saprophagous, detrivorous and bacteria-eating species) were more abundant at low levels of agricultural intensification (i.e. in cereal fields with no or little applications of mineral fertilizers and pesticides located in structurally complex landscapes). This group appeared to have benefited from a higher availability of larval food resources such as decaying plant material, cow dung, ant nests or fungi, respectively, provided by more heterogeneous habitats/landscapes. In our study, however, we are not able to differentiate the effects of agricultural intensification at local and landscape scales as these two factors were simultaneously linked.

Conclusion

In conclusion, the adults of aphidophagous and non-aphidophagous syrphids varied largely between regions and responded differentially to agricultural intensification. Aphidophagous species were more abundant at high levels of AI, while non-aphidophagous species were more abundant at low levels of AI. Moreover, species identity of aphidophagous syrphids regionally changed, thereby resulting in contrasting outcomes in the coincidence with their aphid prey. Future agri-environmental management should, therefore, consider the role of species identity across regions, and contrasting responses of region-specific subsets of syrphid species contributing to biodiversity and biological control.

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Appendix

Appendix S1: Total syrphid numbers for four consecutive sampling dates in Sweden and Germany: early cereal flowering (ef), late cereal flowering (lf), early cereal milk-ripening (emr) and late cereal milk-ripening (lmr).

	Sweden				Germany			
Species	ef	lf	emr	lmr	ef	lf	emr	lmr
Anasimyia contracta[b] (Claussen & Torp) 1980	1		1					
Anasimyia lineata[b] (Fabricius) 1787	1		1					
Anasimyia transfuga[b] (Linnaeus) 1758	1	1						
Cheilosia spec.[b]							9	
Chrysotoxum bicinctum[a] (Linnaeus) 1758				1				
Chrysotoxum latilimbatum[a] Collin 1940					1			
Chrysotoxum verralli[a] (Collin) 1940						1	1	
Dasysyrphus albostriatus[a] (Fallén) 1817							2	1
Epistrophe eligans[a] (Harris) 1780					1			
Episyrphus balteatus[a] (De Geer) 1776	1	1	7	58	76	293	1052	368
Eristalis arbustorum[b] (Linnaeus) 1758					3		1	
Eristalis interrupta[b] (Poda) 1761					1	1		
Eristalis jugorum[b] Egger 1858					3			
Eristalis lineata[b] (Harris) 1776					1			
Eristalis tenax[b] (Linnaeus) 1758					5		2	
Eristalis pertinax[b] (Scopoli) 1763				1				
Eumerus cf. sogdianus[b] (Stackelberg) 1952				2				
Eupeodes corollae[a] (Fabricius) 1794	5	6	11	52	124	193	237	43
Eupeodes lundbecki[a] (Soot Ryen) 1946				1	1			
Ferdinandea cuprea[b] (Scopoli) 1763						1		
Helophilus trivittatus[b] (Fabricius) 1805			1	1		1		
Helophilus pendulus[b] (Linnaeus) 1758				1	1	1	1	
Melanostoma mellinum[a] (Linnaeus) 1758			1	1		1	2	2
Melanostoma scalare[a] (Fabricius) 1794			1	2	1	2	15	10
Pipizella cf. viduata[a] (Linnaeus) 1758				1				
Platycheirus albimanus[a] (Fabricius) 1781		1						
Platycheirus amplus[a] (Curran) 1927					1			
Platycheirus scambus[a] (Staeger) 1843	1							
Rhingia campestris[b] (Meigen) 1822						2		
Scaeva pyrastri[a] (Linnaeus) 1758			1	4	9	10	15	2
Sericomyia nigra[b] (Portchinsky) 1873				1				
Sphaerophoria scipta[a] (Linnaeus) 1758	10	13	54	92	59	41	83	29
Syrphus admirandus[a] (Goeldlin) 1996					6	1		
Syrphus ribesii[a] (Linnaeus) 1758	1			3		11	28	9
Syrphus torvus[a] (Osten-Sacken) 1875					3	6		
Volucella bombylans[b] (Linnaeus) 1758					2	2		
Xylota meigeniana[b] (Stackelberg) 1964	2							
Xylota segnis[b] (Linnaeus) 1758	2	9	15	27	4	7	8	1
Xylota sylvarum[b] (Linnaeus) 1758					1	2	1	

[a] aphidophagous, [b]non-aphidophagous

CHAPTER 4

Landscape context drives crop–non-crop spillover of syrphid flies between hedges, forest edges and adjacent crops

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Teja Tscharntke and Andrea Holzschuh

Abstract

1. Human-dominated landscapes are characterized by a mosaic of natural and managed ecosystems, affecting communities on different spatial scales. Effective landscape management for functionally important organisms suffers from little understanding of organism spillover between semi-natural habitats and adjacent crops, and of how it is affected by the surrounding landscape.

2. We examined syrphid fly abundance (Diptera: Syrphidae) in three types of linear semi-natural habitats differing in the degree of exposure to adjacent crops (n= 35; forest edges, forest-connected and isolated hedges), as well as in the adjacent oilseed rape or winter wheat fields (i.e. altogether n= 70 sites in 35 landscapes). The landscape circles with 1 km radius around the study sites differed in the percentage of oilseed rape (ranging from 0 to 35% oilseed rape) enabling us to test landscape-scale effects of oilseed rape.

3. Aphidophagous syrphids were more abundant in forest-connected hedgerows than in forest edges (with isolated hedges being intermediate), and more abundant in crop fields adjacent to hedgerows than adjacent to forest edges, indicating a preference for hedges over forest edges. Syrphid fly abundance was higher in oilseed rape than in wheat fields. Oilseed rape also enhanced aphidophagous syrphids in adjacent semi-natural habitats, but this effect was modified by the total amount of oilseed rape in the landscape. The abundance of aphidophagous syrphids was only higher adjacent to oilseed rape than adjacent to wheat if the percentage of oilseed rape in the landscape was low (indicating local concentration).

4. *Synthesis and applications*. Our results show that configuration and composition of natural and managed systems can affect syrphid fly communities, including spillover between crop-non-crop habitats. Local spillover from oilseed rape to adjacent semi-natural habitats was only important in landscapes with little oilseed rape, and therefore, little landscape-wide dilution of flower visitors. These complex patterns indicate that conservation measures should take into account the fact that interactions between crops and natural habitat depend on the structure of the surrounding landscape, affecting functionally important groups such as biocontrol agents and pollinators.

Key-words: *oilseed rape, cereals, landscape composition, configuration, concentration, dilution*

Introduction

Human-dominated landscapes are mosaics of cultivated areas interspersed by semi-natural habitats with changing degrees of connectedness, affecting trophic interactions and the spillover across the crop-non-crop interface (Kremen *et al.* 2002; Marshall & Moonen 2002; Tscharntke *et al.* 2005; Rand *et al.* 2006). Hence, conservation of biodiversity and associated ecosystem services such as pollination and biological pest control in agricultural landscapes needs to take configuration and composition of landscapes into account (Tews *et al.* 2004; Holzschuh *et al.* 2007; Fahrig *et al.* 2011; Holzschuh *et al.* 2011).

Landscape-wide conservation of natural habitat has been shown to mitigate the negative effects of agricultural intensification (Altieri 1995; Burel & Baudry 1995), locally maintaining functionally important species pools (Loreau *et al.* 2003). Improving landscape heterogeneity and connectivity can facilitate recolonization of disturbed habitats, counterbalancing locally degraded ecosystem functioning (Fahrig 1997; Elmqvist *et al.* 2003). Linear landscape elements such as forest edges and hedgerows are often the only remaining woody refuges for wildlife in agricultural landscapes (Forman & Baudry 1984). Non-crop habitats can provide resources for natural enemies and pollinating insects such as alternative prey or nectar and pollen resources, shelter from adverse weather conditions or hibernating sites. Spillover of beneficial insect groups from semi-natural habitats to adjacent crops have been reported for many insect groups such ground beetles, lacewings or syrphid flies (Booij *et al.* 1995; Long *et al.* 1998; Bianchi *et al.* 2006; Haenke *et al.* 2009). However, only little is known about the importance of species movements from crops to semi-natural habitats, which can result if both crop and non-crop habitats provide attractive resources (Rand *et al.* 2006, Blitzer *et al.* 2012).

One of the most recent challenges for biodiversity conservation in European agricultural landscapes is the increased area of oilseed rape (*Brassica napus* L.) planted mainly for bio-fuel production. Oilseed rape, as a highly rewarding food resource attracts insect groups providing both services and disservices including bees, syrphid flies, pollen beetles, stem weevils and cabbage aphids (Ferguson *et al.* 2003; Pontoppidan *et al.* 2003; Westphal *et al.* 2009; Jauker *et al.* 2011). Although high amounts of oilseed rape at the landscape scale can enhance pollinators such as bumblebees (Westphal *et al.* 2003), also negative effects such as increased competition for pollinators in nature conservation areas have been recently found (Holzschuh *et al.* 2011).

Syrphid flies are of particular importance in intensively used agricultural landscapes by maintaining and facilitating important ecosystem services such as biocontrol and pollination. Species differentially utilize crop and non-crop habitats, depending on traits such as dispersal abilities or larval and adult food requirements. In this study, we analysed the importance of three linear semi-natural habitat types (forest edges, forest-connected hedges and isolated hedges) and two crop types (oilseed rape and wheat) adjacent to these habitats for aphidophagous and non-aphidophagos syrphid flies along a gradient of oilseed rape proportion in the surrounding landscapes. To the best of our knowledge, it has never been analysed so far how landscape context affects local spillover between crop and non-crop habitats.

We tested the following hypotheses: (i) abundances of syrphid flies differ among semi-natural habitats differing in the degree of exposure to adjacent crops (forest edges, forest-connected hedges and isolated hedges) and these differences among semi-natural habitats also affect syrphid fly spillover between the semi-natural habitats and the adjacent crop fields (ii) abundances of syrphid flies in semi-natural habitats are higher adjacent to oilseed rape than adjacent to wheat, because of higher local spillover from mass-flowering oilseed rape (iii) spillover is more pronounced in landscapes with low than high percentages of oilseed rape, because of landscape-scale dilution of syrphid flies in landscapes with high percentages of oilseed rape (see Fig. 1).

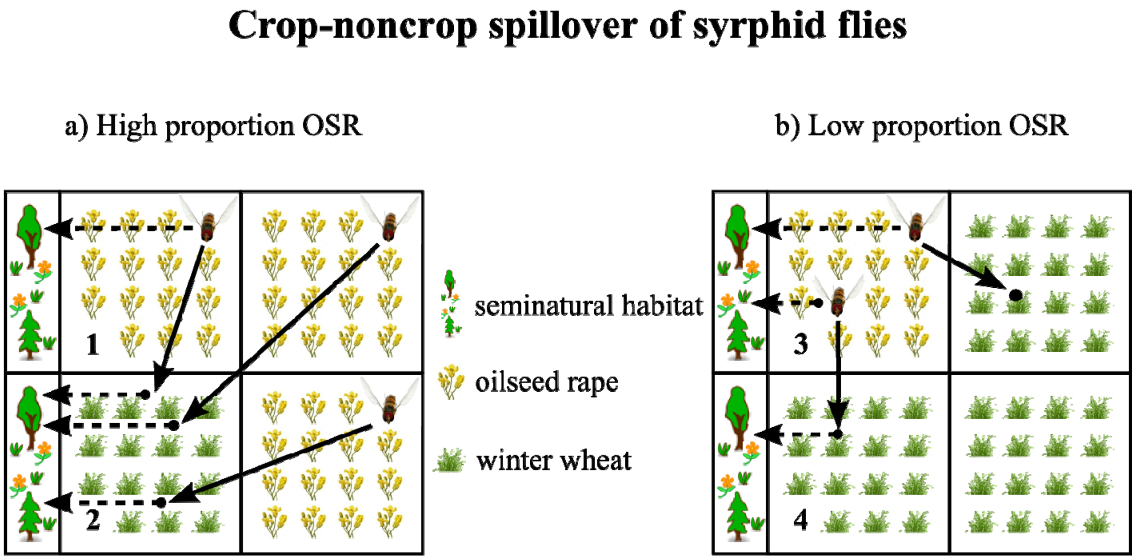

Figure 1: Hypothesized syrphid fly densities (continuous arrows) and local spillover between crop-non-crop habitats (dashed arrows) in situations of high (a) vs. low (b) proportions of oilseed rape at the landscape scale.

(a) In oilseed rape (1), low local syrphid density because of dilution effects across large areas of mass-flowering crops. In winter wheat (2), high local syrphid fly density in landscapes with high proportions of OSR (concentration due to high aphid abundances in wheat), accompanied by high local spillover between the crop-non-crop interface.

(b) In cereal (3), high local syrphid fly density in landscapes with low proportions of OSR (concentration to highly rewarding pollen and nectar availability of OSR), accompanied by high local spillover between the crop–non-crop interface. In winter wheat (4), low local syrphid fly density in landscapes with low proportions of OSR (dilution among wheat fields) accompanied by low local spillover between the crop–non-crop interface.

Materials and methods

Study area and study design

The study was conducted in the vicinity of the city of Göttingen (Appendix S2 Supporting Information; 51·5°N, 9·9°E) in Lower Saxony, Germany, in 2009. The area is dominated by intensive agriculture (c. 75%) with cereal and oilseed rape fields (2-5 ha average field size), interspersed by fragments of semi-natural habitats such as forests, hedgerows and grasslands (Steffan-Dewenter *et al*. 2002). Forest edges and hedges are usually managed by pruning. Forest edges are linear structures like hedges, but adjacent to a forest dominated by deciduous tree species such as the common beech (*Fagus sylvatica* L.). Hedges are isolated linear landscape elements or connected to forest edges. The dominant shrub species in hedges are blackthorn, hawthorn and hip.

We analysed syrphid fly abundance in three types of linear semi-natural habitats, which differed in the degree of exposure to adjacent crops: forest edges (n=12) with little exposure; forest-connected hedgerows (n=12) with intermediate exposure; and isolated hedgerows (n=12) with high exposure. Additionally syrphid fly abundance was analysed in crop fields adjacent to the above-mentioned habitat types (oilseed rape and winter wheat). Half of the replicates of each habitat type (n=6) was located adjacent to oilseed rape fields, whereas the other half was located adjacent to wheat fields (n=6). One study site of forest-connected hedgerow next to wheat had to be excluded, because the farmer refused permission of sampling on his field. Study sites had a minimum distance of 500 metres to each other in order to minimize spatial autocorrelation (Steffan-Dewenter & Tscharntke 1999). Furthermore, the percentage area of oilseed rape (oilseed rape %) around fields within 1 km radius was measured using digital thematic maps (ATKIS DTK 50), complemented by ground checking of crops in the study season (ArcGIS Desktop 10.0).

Sampling of syrphid flies

Syrphid flies were sampled along 200 m long transects by sweep netting located (i) in forest edges and hedgerows (3 stepped method, one sweep per footstep; 1st sweep near the ground, followed by 2nd sweep in medium height and 3rd sweep in maximum reachable height of forest edges and hedgerows) and (ii) in the adjacent crop (oilseed rape or wheat) along 200m long transects located parallel to the forest edges and hedgerows at distances of 6 m from the field boundary. Sampling was carried out two times during oilseed rape flowering in the first half of May (1 per week) and secondly two times during wheat milk-ripening in the first half of June (1 per week). Data were pooled for May and for June. All invertebrates were placed in 3-L plastic bags, killed with diethyl ether, cooled, and then taken to the laboratory. Syrphid flies were separated from all other arthropod taxa and identified, where possible, to species level using identification keys (van Veen 2004). Syrphid species were separated into two trophic groups according to their larval feeding type: aphidophagous feeding type and non-aphidophagous feeding type including saprophagous, detrivourous, bacteriophagous, phytophagous and fungivourous species (a list of syrphids fly species is available in Appendix S1 Supporting Information).

Statistical analyses

Species richness of aphidophagous and non-aphidophagous syrphid flies was highly correlated with their corresponding abundance in semi-natural habitats (aphidophagous species richness: rho= 0·9, p= <0·001; non-aphidophagous species richness: rho= 1·0, p= <0·001) and crops (aphidophagous species richness: rho= 0·9, p= <0·001; non-aphidophagous species richness: rho= 1·0, p= <0·001). Since species richness and abundance analyses showed largely the same pattern we present only the results from the abundance analysis. Abundances of syrphid flies (aphidophagous and non-aphidophagous) were analysed using general linear mixed models (GLMM) with site as random factor to control for the lack of temporal independence between the data from the two sampling dates per site. We performed two separate analyses (i) for semi-natural habitats (data collected from forest edges, forest-connected and isolated hedgerows) and (ii) for crop fields (data collected from oilseed rape and wheat fields). The data from semi-natural habitats tested the influence of (i) oilseed rape % in the surrounding landscape at 1 km radius, (ii) habitat type (forest edges, forest-connected and isolated hedgerows), (iii) adjacent crop type (oilseed rape vs. wheat) and (iv) sampling date (during oilseed rape flowering vs. wheat milk-ripening). With data from crops fields we tested the influence of (i) oilseed rape % in the surrounding landscape at 1 km radius, (ii) adjacent habitat type (forest edges, forest-connected and isolated hedgerows), (iii) crop type (oilseed rape vs. wheat) and (iv) sampling date (during oilseed rape flowering vs. wheat milk-ripening). Model assumptions were tested by examining the Gaussian distribution of the residuals using normal quantile-quantile plots. Data on abundance of syrphid flies was log-transformed to compensate for the skewness and/or kurtosis of the data in order to achieve normally distributed residuals. Models were tested up to three-fold interactions. All non-significant main effects and interactions were excluded from the models using a backward selection procedure. In a second step, we tested model simplifications with maximum likelihood tests in order to gain minimum adequate models. All calculations were done using lme4 package of R version 2.12.1 (R Development Core Team, 2010). Differences between the three semi-natural habitat types were further analysed on the minimal adequate model using Tukey HSD post-hoc tests implemented in the multcomp package (Hothorn *et al*. 2008).

Results

Overview

A total of 47 syrphid species with 526 individuals was collected during the two sampling periods. Syrphid flies predominantly occurred in semi-natural habitats (321) compared to crop fields (205 individuals). The syrphid community was dominated by aphidophagous species (29) and individuals (445). The abundances per syrphid species are given in Appendix S1, Supporting information.

Aphidophagous syrphids

Abundances of aphidophagous syrphid flies in linear semi-natural habitats (SNH) were higher in forest-connected hedgerows than in forest edges with isolated hedges being intermediate (Table 1; dark grey bars in Fig. 2A). Adjacent oilseed rape fields enhanced aphidophagous syrphid fly abundance in the SNH compared to SNH adjacent to wheat, but this effect was modified by the total amount of oilseed rape in the landscape (interaction adjacent crop type × oilseed rape %; Table 1). The positive effect of oilseed rape (i.e. the difference between SNH adjacent to oilseed rape and SNHs adjacent to wheat) decreased with increasing total amount of oilseed rape in the landscape (Fig. 1, Fig. 2B). The abundance of aphidophagous syrphid flies during wheat milk-ripening (date 2) was more than twice as high as during oilseed rape flowering (date 1) (means ± SE: 5·5 ± 1·0 vs. 2·1 ± 0·4).

Abundances of aphidophagous syrphid flies in crop fields were affected by the adjacent type of SNH, with higher numbers in crop fields next to forest-connected and isolated hedgerows than to forest edges (Table 1; dark grey bars in Fig. 2C). Crop type had a marginally significant effect on aphidophagous abundance, which tended to be higher in oilseed rape than in wheat fields (Table 1; grey bars in Fig. 2D).

Non-aphidophagous syrphids

There was only a weak effect of SHN type on non-aphidophagous syrphid abundance, which tended to be lowest in isolated hedges (Table 1, Fig. 2A). Other factors did not affect this functional group in semi-natural habitats (Table 1).

Non-aphidophagous abundance was higher in oilseed rape than in wheat fields (Table 1; light grey bars in Fig. 2D), and higher during oilseed rape flowering (date 1) than during wheat milk-ripening (date 2) when located next to forest edges (interaction: adjacent habitat type × date; Table 1).

Table 1: General linear mixed models relating aphidophagous, non-aphidophagous syrphid fly and wild bee abundance as well as the abundance of *Melanostoma scalare* to four predictive factors. Table shows results for syrphid flies within semi-natural habitats and within crop fields. In semi-natural habitats we tested for (i) oilseed rape %, (ii) habitat, (iii) adjacent crop type and (iv) date. In crop fields we tested for (i) oilseed rape %, (ii) adjacent habitat type, (iii) crop type and (iv) date. F-values and levels of significance resulting from minimum adequate models are given.

	Semi-natural habitat	*F/p*	Crop	*F/p*
SYRPHID ABUNDANCE				
Aphidophagous	rape %	0·0^{NS}	adjacent habitat type	**8·0****
	habitat type	**6·8****	crop type	3·9$^{(*)}$
	adjacent crop type	**8·3****		
	date	**11·4****		
	rape % × adjacent crop type	**4·7***		
Non-aphidophagous	habitat type	3·1^{NS}	adjacent habitat type	0·4^{NS}
			crop type	**4·4***
			date	1·0^{NS}
			adjacent habitat type × date	**4·0***

***P < 0·001; **P < 0·01; *P < 0·05; (*) P < 0·06

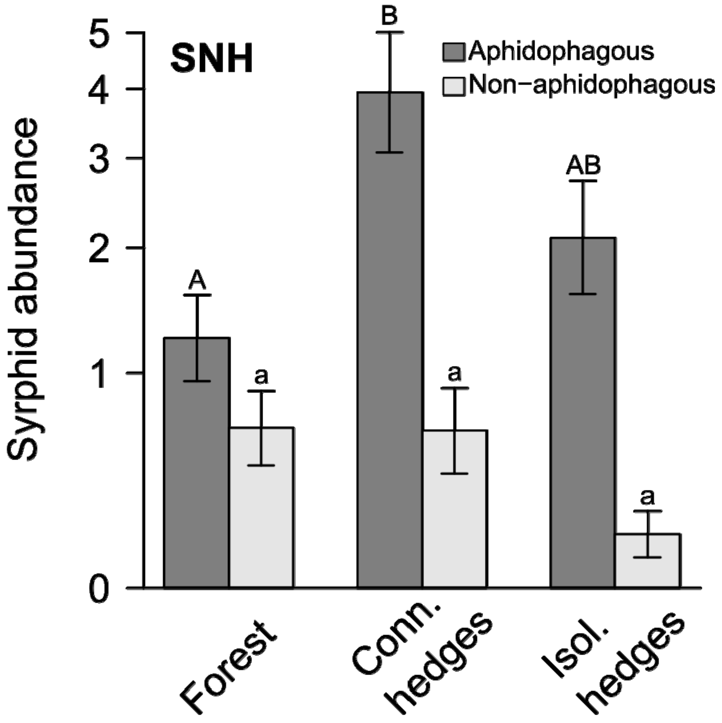

Fig. 2 A: Aphidophagous (dark grey bars) and non-aphidophagous (light grey bars) syrphid fly abundance in semi-natural habitats (SNH); [forest edges (= Forest), forest-connected hedges (= Conn. hedges), isolated hedes (= Isol. hedges)]. Dissimilar capital letters show significant differences. Means and standard errors are given.

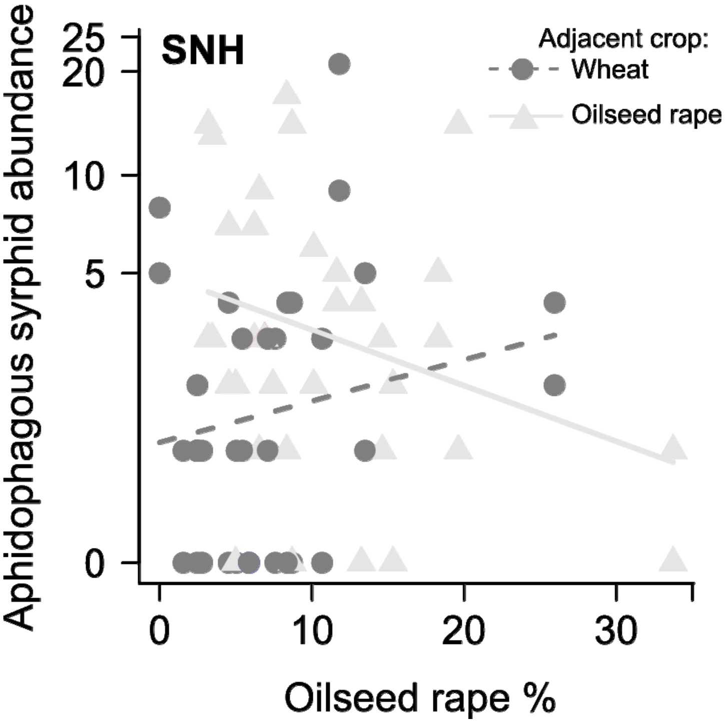

Fig. 2 B: Aphidophagous syrphid fly abundance in semi-natural habitats (SNH) next to (i) oilseed rape fields (solid line) and (ii) wheat fields (dashed line) in relation to percentage of oilseed rape in the surrounding landscape (1 km radius). Lines show GLM model predictions.

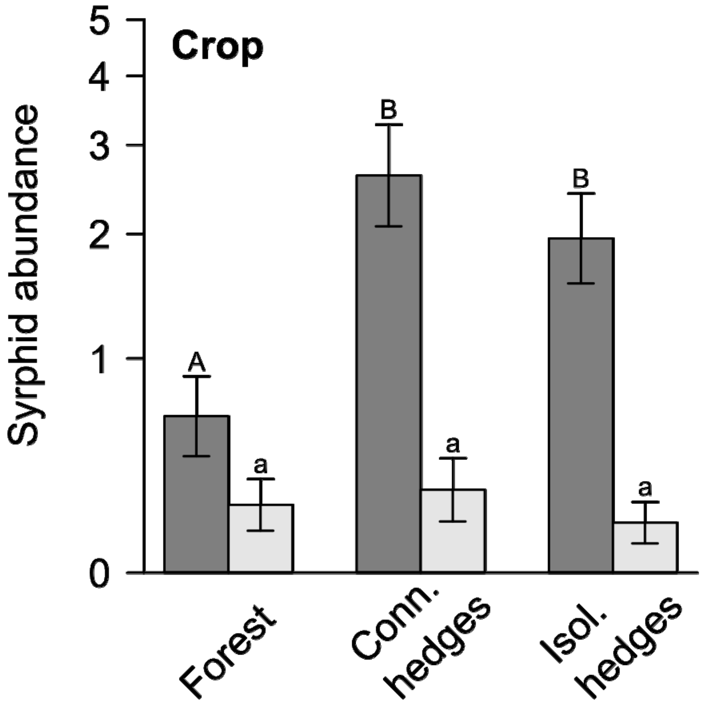

Fig. 2 C: Aphidophagous (dark grey bars) and non-aphidophagous (light grey bars) syrphid fly abundance in crop fields (Crop: winter wheat and oilseed rape fields) next to semi-natural habitats [forest edges (= Forest), forest-connected hedges (= Conn. hedges), isolated hedes (= Isol. hedges)]. Dissimilar capital letters show significant differences. Means and standard errors are given.

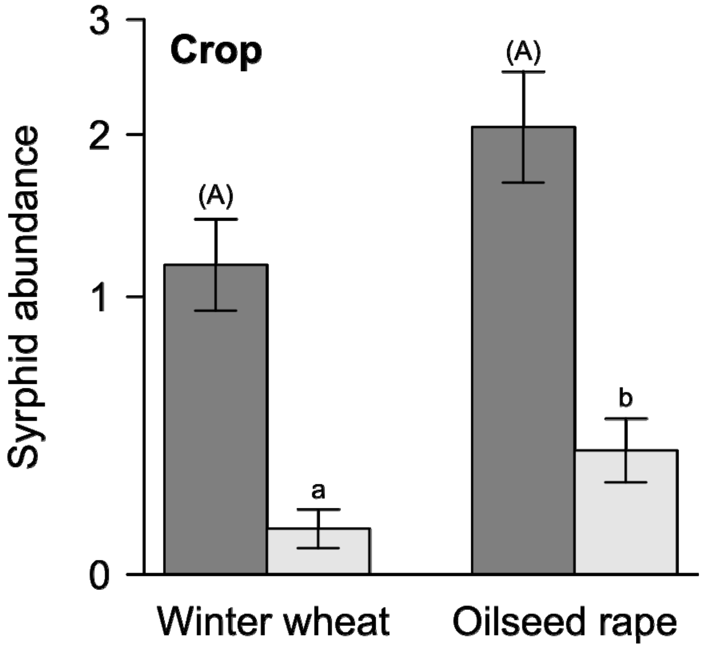

Fig. 2 D: Aphidophagous (dark grey bars) and non-aphidophagous (light grey bars) syrphid fly abundance in winter wheat and oilseed rape fields. Dissimilar capital letters show significant differences. Means and standard errors are given.

Discussion

In this study we examined the effects of three linear semi-natural habitat types (SNH; forest edges vs. forest-connected hedgerows vs. isolated hedgerows) and two cropping systems (wheat vs. oilseed rape fields = OSR) on two groups of functionally important syrphid flies (aphidophagous and non-aphidophagous). Furthermore, we assessed the effects of SNH on adjacent crop habitats and vice versa, and the effects of varying proportions of mass-flowering OSR at the landscape scale (OSR %).

Aphidophagous syrphid abundance was higher in forest-connected hedgerows than in forest edges with isolated hedges showing intermediate abundances. This pattern was mirrored by the adjacent crop fields where abundances were highest adjacent to forest-connected hedgerows and lowest adjacent to forest edges. These parallel patterns in crop fields and adjacent SNH, suggest local spill-over from SNH towards crop fields, taking into account the uniformly lowered abundances in crop fields compared to the abundance in SNH. Furthermore, our results show for the first time that local spill-over across crop non-crop habitat is modified by the amount of OSR at the landscape scale, with possibly strong effects on the success of important ecosystem services such as biological pest control and pollination.

Abundance of both aphidophagous and non-aphidophagous syrphid flies was higher in oilseed rape than in wheat fields, confirming the general idea that functionally important insect guilds can profit from mass-flowering crops that provide huge amounts of pollen and nectar resources (Jauker *et al*. 2011). While the role of wild bees and managed honeybees for crop pollination is comprehensively documented (Corbet *et al*. 1991; Delaplane & Mayer 2000), recently also syrphid flies have been shown to be potentially efficient pollinators of oilseed rape (Jauker & Wolters 2008). Syrphid fly communities were dominated by the aphidophagous larval feeding type, a pattern that is typical in highly intensified land-use systems (Frank 1999; Sadeghi & Gilbert 2000; Haenke *et al*. 2009).

Aphidophagous syrhid flies

Aphidophagous syrphid flies were strongly affected by the type of SNH, showing a distinct preference for forest-connected hedgerows compared to forest edges. Hedgerows in the agricultural matrix are surrounded by arable fields, while forest edges adjoin arable fields at one side only and are often part of a coherent forest patch. Although syrphid flies often use forest edges as overwintering habitats (Hondelmann & Poehling 2007), they find their laval prey mainly in arable fields (Meyer *et al.* 2009). Jauker *et al.* (2008) showed even increasing aphidophagous syrphid fly abundances with increasing distance from SNH. The larger open-land area around hedgerows compared to around forest edges provides a larger habitat area for larval and adult syrphid fly feeding (aphids in wheat and nectar and pollen resources in OSR fields) in the vicinity of hedgerows than of forest edges. In turn, this could have increased the attractiveness of hedgerows – compared to forest edges – as resting sites or places for alternative food resources.

The results of this study clearly show the prominent importance of SNH type for generalist aphidophagous syrphid flies, both within the SNH and also in the adjacent crop systems. SNH thereby can play an important role in temporarily maintaining functionally important aphidophagous syrphid flies within the agricultural matrix, being even more relevant than rewarding crop plants such as mass-flowering oilseed rape and winter wheat used as resources for adult and larval feeding. Resembling the situation for generalist butterflies, aphidophagous syrphid flies seem to similarly benefit from convenient microclimate conditions, lowered anthropogenic disturbance and possibly, additional biotic resources and shelter from predators, allowing for facilitated access to highly rewarding arable fields (OSR and wheat) (Scalercio *et al.* 2007).

This study shows that mass-flowering OSR can have positive effects on the abundance of aphidophagous syrphid flies in nearby SNH, with increased abundances in SNH next to OSR fields. This finding resembles the situation for bumblebees, which exhibit strongly increased visitation rates of flowering wild plants in SNH adjacent to mass-flowering field bean fields (Hanley *et al.* 2011). The most significant new finding of the present study is that the landscape-scale amount of mass-flowering crops such as OSR apparently modify spill-over processes between non-crop and crop habitats. This landscape effect of OSR was found to be independent from the date of sampling (non significant three-way interaction: OSR % × SNH type × date of sampling) indicating that varying oilseed rape proportions, even after the main flowering period, may still play an important role for aphidophagous syrphid flies, possibly due to additional wild flowering plants or alterative aphid resources. Hence, aphidophagous syrphid abundances were increased in SNH adjacent to OSR fields, but only in landscapes with low proportions of OSR at the landscape scale. Contrastingly, this difference between aphidophagous syrphid abundances in SNH adjacent to OSR and adjacent to wheat fields declined at high proportions of OSR at the landscape scale.

This interesting pattern is obviously a result of differing OSR availabilities at the landscape scale, resulting in specific patterns of abundance depending on local crop systems. Thus aphidophagous syrphid flies with their excellent flight and vision abilities (Lunau & Wacht 1994; Sutherland *et al*. 2001) can easily detect SNH neighbouring remote OSR fields in landscapes with low OSR proportions, leading to a concentration of syrphid flies in nearby SNH, whereas in situations with high OSR proportions, only low abundances are observable. This finding suggests that at high OSR proportions, local abundances in SNH and OSR fields are low due to landscape wide dilution of syrphid flies among sweepingly available oilseed rape fields. Landscape-scale effects such as dilution of functionally important insect guilds are poorly understood, but should often be responsible for negative effects on maintaining important ecosystem services such as pollination and biological control in crops used, but also in conservation sites (Tscharntke *et al*. 2012). Holzschuh *et al*. (2011) showed that increasing amounts of oilseed rape at the landscape scale can lead to an increased competition for pollinators between endangered wild-flowering plants and crops. Such negative effects on wild plant reproduction may also occur in the SNH investigated in this study, thereby possibly also affecting higher taxa such as overwintering farmland birds and small mammals, which depend on fruit bearing shrubs in forest edges and hedgerows (Siriwardena *et al*. 2008).

Contrasting to the situation in SNH, a landscape effect of OSR on local aphidophagous syrphid abundances within crop fields was not found. This may indicate that crop fields compared to SNH are only temporarily used habitats for adult feeding and oviposition, resulting in a high variability and low abundances, thereby explaining only marginally increased aphidophagous abundances in OSR compared to wheat fields.

Non-aphidophagous syrphid flies

In contrast to the results for aphidophagous syrphid flies, non-aphidophagous larval feeding types were affected by SNH type and crop type only in SNH adjacent crops, but not in the SNH themselves. They increased in OSR fields with higher abundances next to forest edges during the OSR flowering period.

Compared to aphidophagous syrphid flies, this minor importance of semi-natural habitats is possibly a result of the different reproduction strategy of non-aphidophagous syrphid flies. While aphidophagous flies can find suitable aphid species for larval feeding in crop fields as well as in hedgerows and forest edges, most of the non-aphidophagous syrphid species found in this study belong to the genus *Eristalis* depending on aquatic habitats (van Veen 2004), which are widely absent in the investigated woody structures. However, non-aphidophagous abundances were increased in oilseed rape fields providing huge amounts of pollen and nectar resources, thereby indicating large-scale foraging behaviour of this highly mobile syrphid fly group. Forest edges positively influenced non-aphidophagous syrphid abundance in adjacent crop fields during oilseed-rape flowering. This temporal pattern appears ambiguous, but may be explained by an increased overwintering success of non-aphidophagous syrphid flies in forest edges, compared to openland habitats such as hedgerows, whereas later in the year, large-scale migration to foraging and ovipositioning sites becomes increasingly important. Thus non-aphidophagous syrphid flies, although apparently benefiting from mass-flowering crops such as oilseed rape, appear to be less adapted to intensively used agricultural landscape than the group of generalist aphidophagous syrphid flies.

Conclusion

Biodiversity in highly intensified land-use systems is of crucial importance for both maintaining important ecosystem services and improving resilience against spatial and temporal changes in landscape composition (Bengtsson *et al*. 2003). We show how linear landscape elements such as hedgerows attract beneficial aphidophagous syrphid flies, thereby possibly contributing to the augmentation of biological control potential in highly intensified land-use systems. Furthermore, our results indicate that aphidophagous syrphid fly are influenced by the amount of oilseed rape at the landscape scale, mediating local spill-over processes between crop-non-crop habitats (dilution and concentration effects). Effective habitat schemes for beneficial arthropods should not only focus on the local configuration of crop and non-crop habitat, but also take into account the influence of changing amounts of crop type, in particular mass-flowering crops, at the landscape scale.

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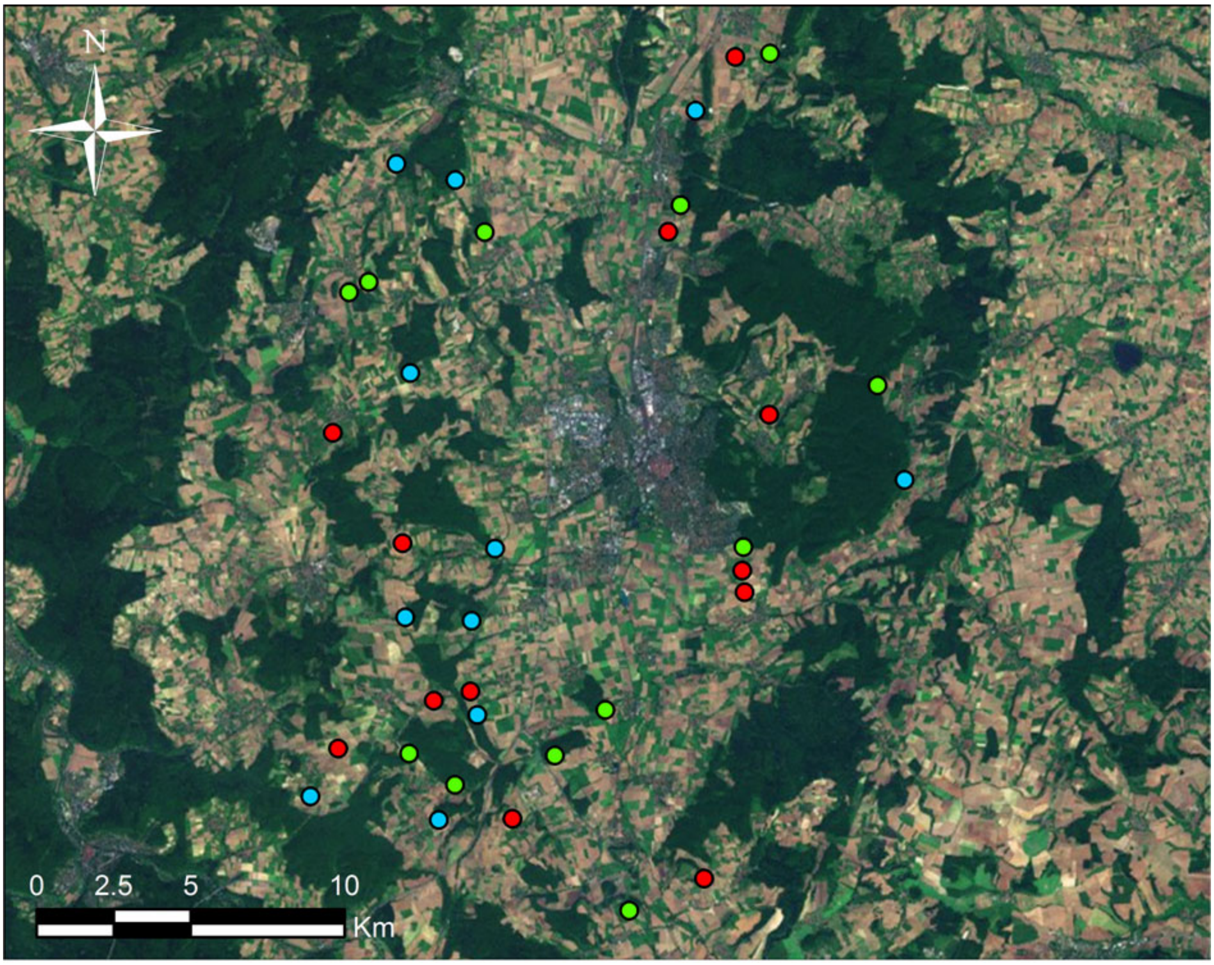
Appendices

Appendix S 1: Syrphid numbers in semi-natural habitats (forest edges=F; forest-connected hedges=C; isolated hedges=I) and in adjacent crop. Means ± standard errors per site and sampling date are given. [a] shows aphidophagous and [b] non-aphidophagous syrphid species.

Syrphid species	Wheat			Oilseed rape		
	F	C	I	F	C	I
Baccha elongata [a] (Fabricius, 1775)	0·00 ± 0·00	0·05 ± 0·05	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·04 ± 0·04
Chamaesyrphus lusitanicus [a] Mik, 1898	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·08 ± 0·08	0·00 ± 0·00	0·00 ± 0·00
Cheilosia spec. [b]	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·04 ± 0·04	0·04 ± 0·04	0·00 ± 0·00
Cheilosia mutabilis [b] (Fallén, 1817)	0.00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00
Cheilosia vicina [b] (Zetterstedt, 1849)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00
Chrysogaster virescens [b] Loew, 1854	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00
Chrysotoxum bicinctum [a] (Linnaeus, 1758)	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00
Chrysotoxum cautum [a] (Harris, 1776)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00
Dasysyrphus hilaris [a] (Zetterstedt, 1843)	0·00 ± 0·00	0·05 ± 0·05	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00
Dasysyrphus venustus [a] (Meigen, 1822)	0·00 ± 0·00	0·05 ± 0·05	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00
Epistrophe eligans [a] (Harris, 1780)	0·00 ± 0·00	0·05 ± 0·05	0·17 ± 0·10	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00
Epistrophe melanostoma [a] (Zetterstedt, 1843)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00
Epistrophe nitidicollis [a] (Meigen, 1822)	0·04 ± 0·04	0·05 ± 0·05	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04
Episyrphus balteatus [a] (De Geer, 1776)	0·17 ± 0·08	0·60 ± 0·21	1·00 ± 0·27	0·04 ± 0·04	0·50 ± 0·22	0·50 ± 0·20
Eristalis spec. [b]	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·21 ± 0·13	0·00 ± 0·00
Eristalis interrupta [b] (Poda, 1761)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00
Eristalis jugorum [b] Egger, 1858	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00
Eristalis pertinax [b] (Scopoli, 1763)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00	0·13 ± 0·09
Eristalis tenax [b] (Linnaeus, 1758)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·08 ± 0·08	0·00 ± 0·00
Eumerus ornatus [b] Meigen, 1822	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·08 ± 0·08	0·00 ± 0·00	0·00 ± 0·00
Eupeodes corollae [a] (Fabricius, 1794)	0·08 ± 0·06	0·10 ± 0·07	0·13 ± 0·07	0·08 ± 0·08	0·46 ± 0·26	0·04 ± 0·04
Eupeodes latifasciatus [a] (Macquart, 1829)	0·00 ± 0·00	0·05 ± 0·05	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00
Heringia heringi [a] (Zetterstedt, 1843)	0·00 ± 0·00	0·05 ± 0·05	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00
Melanostoma spec. [a]	0·00 ± 0·00	0·10 ± 0·10	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00
Melanostoma mellinum [a] (Linnaeus, 1758)	0·08 ± 0·06	0·35 ± 0·15	0·13 ± 0·07	0·00 ± 0·00	1·13 ± 0·61	1·25 ± 0·63
Melanostoma scalare [a] (Fabricius, 1794)	0·33 ± 0·13	1·30 ± 0·89	0·46 ± 0·15	1·42 ± 0·40	2·92 ± 0·67	1·54 ± 0·42
Melangyla triangulifera [a] (Zetterstedt, 1843)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·04 ± 0·04
Microdon mutabilis / myrmicae [b]	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00
Neoascia podagrica [b] (Fabricius, 1775)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00
Paragus haemorrhous [b] Meigen, 1822	0·08 ± 0·06	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04
Parasyrphus spec. [a]	0·00 ± 0·00	0·05 ± 0·05	0·00 ± 0·00	0·04 ± 0·04	0·04 ± 0·04	0·00 ± 0·00
Pipiza fenestrata Meigen, 1822	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00
Platycheirus albimanus [a] (Fabricius, 1781)	0·00 ± 0·00	0·20 ± 0·20	0·04 ± 0·04	0·13 ± 0·07	0·13 ± 0·09	0·04 ± 0·04
Platycheirus spec. [a]	0·00 ± 0·00	0·10 ± 0·07	0·00 ± 0·00	0·08 ± 0·06	0·13 ± 0·07	0·38 ± 0·18
Platycheirus ambiguus [a] (Fallén, 1817)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04
Platycheirus clypeatus [a] (Meigen, 1822)	0·00 ± 0·00	0·30 ± 0·18	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04
Platycheirus europaeus [a] (Maibach & Speight, 1990)	0·00 ± 0·00	0·20 ± 0·16	0·08 ± 0·06	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00
Platycheirus immaculatus [a] Ohara, 1980	0·00 ± 0·00	0·05 ± 0·05	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00
Platycheirus parmatus [a] Rondani, 1857	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·04 ± 0·04
Platycheirus peltatus [a] (Meigen, 1822)	0·00 ± 0·00	0·05 ± 0·05	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·08 ± 0·08
Platycheirus podagratus [a] (Zetterstedt, 1836)	0·00 ± 0·00	0·05 ± 0·05	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00
Platycheirus scutatus [a] (Meigen, 1822)	0·00 ± 0·00	0·05 ± 0·05	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04
Rhingia campestris Meigen, 1822	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·25 ± 0·11	0·04 ± 0·04	0·04 ± 0·04
Sphaerophoria scripta [a] (Linnaeus, 1758)	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·50 ± 0·22	0·21 ± 0·08
Sphaerophoria taeniata [a] (Meigen, 1822)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·04 ± 0·04
Sphegina clavata [b] (Scopoli, 1763)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00
Syritta pipiens [b] (Linnaeus, 1758)	0·25 ± 0·11	0·05 ± 0·05	0·13 ± 0·13	0·21 ± 0·10	0·71 ± 0·29	0·00 ± 0·00
Volucella bombylans [b] (Linnaeus, 1758)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00
Xanthogramma laetum [a] (Fabricius, 1794)	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00
Xanthogramma pedissequum [a] (Harris, 1776)	0·00 ± 0·00	0·05 ± 0·05	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00
Xylota abiens [b] Meigen, 1822	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·00 ± 0·00	0·00 ± 0·00
Xylota segnis [b] (Linnaeus, 1758)	0·00 ± 0·00	0·00 ± 0·00	0·00 ± 0·00	0·04 ± 0·04	0·04 ± 0·04	0·00 ± 0·00
Syrphinae unidentified	0·04 ± 0·04	0·10 ± 0·07	0·08 ± 0·06	0·04 ± 0·04	0·08 ± 0·06	0·04 ± 0·04

[a] aphidophagous; [b] non-aphidophagous

Appendix S 2: Location of the study sites around the city Göttingen, using ESRI World Imigary. Each dot represents a study site (green: forest edge, blue: connected hedge, red: isolated hedge).



Summary

During the last decades, agriculture has transformed into highly effective and economically optimized production systems with extended cultivation areas and increased usage of fertilizers and pesticides. This development is accompanied by the loss and fragmentation of remaining semi-natural habitats, thereby negatively affecting farmland biodiversity, resulting in species loss and declining ecosystem services such as biological pest control, and pollination. Agri-environmental schemes such as organic farming practices and habitat management can help to mitigate these negative effects, while it is increasingly recognised that attention should be paid to both local and landscape scales. Improving habitat diversity on the landscape scale can enhance biodiversity at the local scale, compensating for intensified local land use.

In this thesis, we analysed the effects of local habitat management (sown flower strips, forest edges and hedges) and farming practices (extensive vs. intensive management) on syrphid fly guilds. In addition, we focused on the influence of landscape scale parameters such as the proportion of arable land as well as the proportion of mass-flowering oilseed rape in the surrounding of study sites.

Syrphid flies represent one of the biggest groups of the order Diptera and occur in a wide range of habitats in agricultural landscapes. While adult syrphids flies are pollen and nectar feeders, their larvae show different feeding strategies ranging from predators of aphids, bacteria feeders and phytophagous to fungivorous species. Aphidophagous species such as *Episyrphus balteatus* or *Sphaerophoria scripta* represent the most frequently occurring syrphid fly species in agricultural landscapes, preying on a wide range of aphids species (e.g. *Sitobion avenae*, *Rhopalosiphum padi*, *Metopolophium dirhodum*), and can play an important role in the suppression of cereal aphid outbreaks.

Here, we studied the effect of naturally occurring grassy strips and sown flower strips on syrphid flies in winter wheat fields, which were located along a gradient of landscape complexity (ranging from 30 to 100 % arable land and at multiple spatial scales ranging from 0.5 to 4 km radii). Analyses on the impact of extensive vs. intensive farming practices on syrphid flies were carried out in two European countries (South-Sweden and North-Germany), in each region by comparing four fields at low and four fields at high levels of agricultural intensification. In addition, syrphid flies were analysed by comparing forest edges, forest-connected hedges and isolated hedges adjacent to crop fields (winter wheat and oilseed rape) with respect to the influence of varying proportions of oilseed rape at the landscape scale.

The results showed that sown flower strips increased syrphid fly abundance. Syrphid species richness was increased in wheat fields adjacent to sown flower strips. Furthermore, species richness and abundance of syrphid flies in sown flower strips increased as the proportion of arable land in the surrounding landscape increased, indicating a local concentration effect to highly rewarding pollen and nectar resources.

Total and aphidophagous syrphid abundances were generally higher in the German than the Swedish study region. Aphidophagous syrphid abundance was higher in high intensity managed fields being located in landscapes with high proportions of arable land, while non-aphidophagous syrphid flies showed higher abundances in low intensity managed fields being located in landscapes with low proportions of arable land. Furthermore, syrphids in the German region appeared earlier in the season, therewith possibly allowing for a better predator-prey synchronization.

Syrphid flies appeared to profit from high amounts of pollen and nectar resources in oilseed rape fields. Aphidophagous syrphid abundance in hedges and forest edges showed contrasting responses to the neighbouring crop, with low abundance when neighboured by oilseed rape fields (dilution) and higher abundance when neighboured by winter wheat fields (concentration) at high proportions of oilseed rape fields at the landscape scale. Aphidophagous syrphid fly abundance was increased in forest-connected hedges as well as in crop fields which lay adjacent to forest-connected hedges, indicating noncrop-crop spillover with potentially positive effects on local bicontrol potential.

In conclusion, results showed that local habitat management can enhance diversity and abundance of syrphid flies, thereby potentially improving local biological control of cereal aphids. On the landscape scale, results support the idea that environmental schemes are more effective in structurally simple compared to complex landscapes owing to the concentration of highly dispersive organisms such as syrphid flies in resource-rich habitats. The relative abundance of aphidophagous syrphids varied largely between German and Swedish study regions indicating a changing role of species identity along latitudes. Syrphid fly guilds (aphidophagous vs. non-aphidophagous) were contrastingly affected by management type (extensive vs. intensive farming). Aphidophagous syrphid fly abundance in semi-natural habitats is mediated by the percentage of oilseed rape at the landscape scale, depending on local crop identity. The positive influence of forest-connected hedges on syrphids calls for group-specific habitat management practices in order to enhance biodiversity and related important ecosystem services such as biological pest control and pollination in the agricultural landscape.

Zusammenfassung

Während der letzten Jahrzehnte hat sich die Landwirtschaft grundlegend verändert und wird heute zunehmend von hocheffektiven, wirtschaftlich optimierten Produktionssystemen mit ausgedehnten Anbauflächen und dem damit verbundenen gesteigertem Einsatz von Kunstdüngern und Pestiziden geprägt. Diese Entwicklung bedingt jedoch auch den Verlust und die Fragmentierung von naturnahen Habitaten mit negativen Auswirkungen auf die Artenvielfalt in intensiv genutzten landwirtschaftlichen Gebieten. Der Rückgang der Artenvielfalt führt zur Schwächung von Ökosystemfunktionen wie der biologischen Schädlingskontrolle oder der Bestäubung von Ackerkulturen. Agrarumweltprogramme, ökologische Anbaumethoden und Habitatmanagement können helfen, diese negativen Auswirkungen abzumildern. Hierbei wird zunehmend deutlich, dass neben der lokalen Ebene auch der Einfluß der strukturellen Diversität auf der Landschaftsebene berücksichtigt werden muß: Eine Steigerung der Habitatdiversität auf der Landschaftsebene kann die Biodiversität auf der lokalen Ebene erhöhen, und so die negativen Folgen einer intensivierten Landnutzung kompensieren.

In dieser Arbeit wurden die Effekte von lokalem Habitatmanagement (künstlich angelegte Blühstreifen, Waldränder und Hecken) und die Effekte verschiedener Anbaumethoden (extensive im Gegensatz zu intensiver Nutzung) auf Schwebfliegen-Gilden untersucht. Des Weiteren wurde der Einfluß bestimmter Landschaftsparameter, wie das Verhältnis von landwirtschaftlich genutzter Fläche zu naturnahem Habitat (als Maß der strukturellen Komplexität der Landschaften), oder der prozentuale Anteil von Rapskulturen im Umfeld der Versuchsflächen untersucht. Schwebfliegen stellen eine der größten Gruppen der Insektenordnung Diptera dar und kommen in vielen verschiedenen Habitaten in landwirtschaftlich genutzten Gebieten vor. Während adulte Schwebfliegen hauptsächlich Pollen- und Nektarkonsumenten sind, zeigen ihre Larven eine große Vielfalt von Ernährungsstrategien, die von zoophagen über bakteriophage und phytophage bis hin zu fungivoren Spezies reichen. Aphidophage Spezies wie *Episyrphus balteatus* oder *Sphaerophoria scripta* stellen die im Untersuchungsgebiet die am häufigsten vertretenen Schwebfliegenarten dar und können eine wichtige Rolle bei der biologischen Schädlingskontrolle verschiedener Blattlausarten einnehmen (z.B. *Sitobion avenae*, *Rhopalosiphum padi*, *Metopolophium dirhodum*).

In dieser Arbeit haben wir den Einfluß künstlich angelegter Blühstreifen und natürlich entwickelter Grasstreifen auf Schwebfliegenpopulationen in Winterweizenfeldern

untersucht, die entlang eines Gradienten der Landschaftskomplexität (zwischen 30% und 100% Ackerland auf mutiplen räumlichen Skalen von 0.5 bis 4 km Radien der Landschaftssektoren) lagen. Die Analyse des Einflusses extensiver im Vergleich zu intensiver Landwirtschaft wurde in zwei europäischen Ländern durchgeführt (Südschweden und Norddeutschland), indem jeweils vier Felder mit hoher landwirtschaftlicher Intensivierung (lokalisiert in strukturarmen Landschaften) mit vier Feldern mit niedriger landwirtschaftlicher Intensivierung (lokalisiert in strukturreichen Landschaften) verglichen wurden. Weiterhin wurde der Einfluß von Waldrändern, mit Waldrädern verbundenen Hecken und isolierten Hecken, die an landwirtschaftliche Flächen (Winterweizen- und Rapsfelder) angrenzten, im Zusammenhang mit veränderlichen Anteilen von Rapsfeldern in der umliegenden Landschaft im Hinblick auf die Häufigkeit von Schwebfliegen untersucht.

Die Ergebnisse haben gezeigt, dass Blühstreifen die Häufigkeit von Schwebfliegen steigern können: Die Schwebfliegen-Artenvielfalt in Weizenfeldern, die sich in der Nähe von Blühstreifen befanden, war ebenfalls erhöht. Weiterhin nahmen der Artenreichtum und die Häufigkeit von Schwebfliegen in den Blühstreifen zu, wenn der Anteil von Ackerland im umgebenden Landschaftsausschnitt anstieg, was zu einer Konzentration von Schwebfliegengemeinschaften auf den vereinzelten, aber als Nahrungsressource lohnenden, Blühstreifen führte.

Die Gesamthäufigkeit von Schwebfliegen, ebenso wie die Häufigkeit von aphidophagen Schwebfliegen, war auf den deutschen Versuchsflächen höher als auf den schwedischen Versuchsflächen. Die Häufigkeit von aphidophagen Schwebfliegen war in Feldern mit hoher Intensivierung erhöht, während nicht-aphidophage Schwebfliegen in Feldern mit niedriger Intensivierung häufiger waren. Außerdem tauchten Schwebfliegen in der deutschen Versuchsregion früher in der Saison auf, was möglicherweise eine engere Räuber-Beute-Synchronisation ermöglicht.

Die Abundanz der Schwebfliegen war in Rapsfeldern im Vergleich zu Weizenfeldern erhöht. Die Häufigkeit von aphidophagen Schwebfliegen in Hecken und Waldrändern unterschied sich entsprechend benachbarter Feldfrüchte (Weizen und Raps) und dem Anteil von Rapsfeldern in der umgebenden Landschaft. Hierbei zeigte sich eine verringerte Abundanz aphidophager Schwebfliegen in der Nachbarschaft von Rapsfeldern (Verdünnungseffekt) und eine erhöhte Abundanz in der Nachbarschaft von Winterweizenfeldern (Konzentrationseffekt) bei gleichzeitig hohen Anteilen von Rapsfeldern in der umgebenden Landschaft. Die Abundanz von aphidophagen

Schwebfliegen war am höchsten in Hecken, welche mit einem Waldrand verbunden waren. Gleichzeitig zeigte sich auch eine erhöhte Abundanz in den an solche Standorte angrenzenden Agrarflächen, was auf ein gesteigertes Übertreten (spillover) zwischen den Hecken-Habitaten und den angrenzenden landwirtschaftlichen Flächen hindeutet, und auf diesem Wege möglicherweise auch die biologische Schädlingskontrolle und die Bestäuberleistung verbessern kann.

Im Allgemeinen haben die Resultate gezeigt, dass lokales Habitatmanagement die Diversität und die Häufigkeit von Schwebfliegen erhöhen kann und dabei möglicherweise auch die biologische Kontrolle von Getreideblattläusen gesteigert werden kann. Auf der Landschaftsebene unterstreichen die Resultate die Annahme, dass Umweltmanagement in strukturarmen Landschaften aufgrund der Konzentration hochmobiler Schwebfliegen in ressourcenreichen Habitaten effektiver ist als in Landschaften mit generell erhöhter Habitattypendiversität. Die relative Häufigkeit von aphidophagen Schwebfliegen variierte stark zwischen der deutschen und der schwedischen Versuchsregion, was auf eine veränderliche Rolle bestimmter Arten in unterschiedlichen Breiten hinweist. Schwebfliegen-Gilden (aphidophage im Gegensatz zu nicht-aphidophagen) wurden unterschiedlich von der landwirtschaftlichen Intensivierung beeinflußt. Die Häufigkeit von aphidophagen Schwebfliegen in naturnahen Hecken wird durch den Prozentsatz der Rapsfelder in der umgebenden Landschaft sowie die Art der benachbarten Feldfrüchte beeinflußt. Die positive Wirkung seminatürlicher Habitate wie künstlicher Blühstreifen und Hecken auf angrenzende Anbauflächen (mit veränderlicher Stärke entsprechend verschiedener Landschaftsparameter wie Ackeranteil und Rapsanteil) zeigt den dringenden Bedarf an gruppenspezifischen Habitatmanagementmethoden, um die Biodiversität und damit verbundene Ökosystemleistungen wie die biologische Schädlingskontrolle und Bestäubung in Agrarlandschaften zu verbessern.

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Curriculum vitae

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Thesis declarations

The Chapters 2 to 4 are a series of manuscripts that have or will be submitted to peer - reviewed journals. I am the overall author of all manuscripts presented in this thesis. Development of main ideas, data collection, statistical analysis and writing of the manuscripts is my original work. The respective co-authors contributed to various parts of the studies and provided comments to the manuscripts.

Hereby I confirm that I have written this doctoral thesis independently, that I have not used other sources or facilities than the ones cited and acknowledged, that I have not used unauthorized assistance and that I have not submitted this thesis previously in any form for another degree at any university or institution.

Göttingen, Februar 2012

Sebastian Hänke